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HYBRID OAKS OF NORTH AMERICA

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THE RECORDED HISTORY of American hybrid oaks begins with the publication (36) of a description of \times *Quercus heterophylla* by François André Michaux in 1812. The short Latin description and notes and the excellent colored plate in his *Silva* give a very good idea of the general characters of the plant. It was believed by Michaux to be a distinct species, but he made the significant statement that it was known only from a single stock on the banks of the Schuylkill River in a field belonging to Mr. Bartram. The plant was later propagated by seeds and cuttings from the original tree and so found its way into a number of botanic and private gardens. There was much debate among early botanists as to whether it was a species or a hybrid, and there has been some difference of opinion as to the identity of the parent species among those who regarded it as a hybrid. All writers seem to have agreed that the willow-oak was one of the parents, but the northern red oak, the black oak, scarlet oak, pin-oak, and Spanish oak (*Quercus falcata*) have all been suggested as the other parent. It is now generally regarded as a cross between the willow-oak (*Quercus Phellos*) and the northern red oak (*Q. borealis*).

Scattered trees discovered in different parts of the country in recent years have been referred to \times *Quercus heterophylla* on account of a general resemblance in foliage. There is no reason to doubt that many of these hybrids were identical in parentage with Bartram's oak, but some of them were probably of a different hybrid origin. The controversy over this interesting oak was probably due rather to the conservatism of the early botanists and to their philosophical or theological bias in regard to species than to lack of internal evidence in the material.

Thomas Nuttall described \times *Quercus Leana* in 1919 (41), giving a clear description and a good plate as well as a rather full discussion of the tree. He pointed out its similarity to \times *Quercus heterophylla* but concluded from a study of material with mature fruit that it was "either a distinct species or another strange hybrid." Mr. Thomas G. Lea, the discoverer of the tree near Cincinnati, Ohio, expressed the opinion in notes quoted by

Nuttall that it was a hybrid, most likely between *Quercus imbricaria* and *Q. velutina* or *Q. coccinea*. Nuttall expressed a doubt, however, as to whether such mixed races occur spontaneously in nature; and so he rather discounted Lea's shrewd and correct surmise as to its origin and relationship and decided to publish it as a species. This hybrid has since turned up at a number of widely scattered stations and it has been brought into cultivation in botanic gardens both in America and in Europe. It seems to be one of the most frequent of natural hybrids, and it may be looked for wherever the shingle-oak and black oak grow in proximity to each other.

In 1863 Dr. Albert K. Kellogg, a keen amateur botanist of California, published a description of \times *Quercus Mohreus* (31). This tree was also believed to be a distinct species by the author; but it has since been shown that it is without much doubt a hybrid between *Quercus Kelloggii* and *Q. Wislizeni*.

Dr. George Engelmann was the first American botanist to pay particular attention to spontaneous hybrids among the oaks and to publish notes on them. In a paper presented to the Academy of Science of St. Louis in 1876 (24) he enumerated ten hybrids that he considered well authenticated. Engelmann did not propose any strictly new names for the hybrid oaks, but he recognized the hybrid character of \times *Quercus heterophylla* and \times *Q. Leana*, and he believed *Quercus sinuata* Walter¹ to be a hybrid between the species now known as *Quercus laevis* and *Q. nigra*. He also adopted the name \times *Quercus tridentata* for the cross between *Q. imbricaria* and *Q. marilandica*. This was based on *Quercus nigra* (*marilandica*) *tridentata* A. DC. Only the names of the supposed parent species were given in discussing the other six hybrids. Three of the hybrids recognized by Engelmann were between white oak species and seven between black oaks.

Several interesting points were brought out by Engelmann in the general discussion. He mentioned the difficulty of dealing with the question of hybridity in plants when the character of sterility fails, as it was stated, is the case with the oaks where the seeds "come true" and do not revert to the parent forms. White and black oaks, he observed, are too distinct to be crossed; among the white oaks, hybrids appear to be much rarer than among the black oaks—or it may be that they are merely more difficult to recognize; the seeds appear to be as fertile as in true species, but at the same time they do not seem to propagate themselves or to spread in their native woods.

After the publication of Engelmann's paper it began to be recognized among American botanists that natural hybrids do occur between certain species of oaks.

In 1882 Dr. N. L. Britton described \times *Quercus Rudkinii* (10) from specimens collected near Keyport, N. J. This was regarded as a hybrid

¹ The name \times *Quercus Walteriana* was later proposed by Ashe (5) for this hybrid on the ground that *Q. sinuata* Walt. was, in his opinion, the earliest name for the species described by Small in 1903 as *Quercus austrina*.

between *Quercus marilandica* and *Q. Phellos*. Other trees supposed to be of the same mixed parentage have since been discovered on Staten Island, N. Y., and at a number of other stations from North Carolina and Florida to Texas. Several other hybrid oaks were discovered during the next quarter of a century and some of them were given binomials by authors who either recognized their hybrid character or regarded them as new species.

Dr. William Trelease entered the field in 1917 with a paper on naming hybrid oaks (64). In the introduction he called attention to the fact that two methods of designating plant hybrids were approved by the Botanical Congresses of Vienna and Brussels — one by giving the names of the parent species separated by the conventional \times sign; the other by using a binomial preceded by the same sign. In discussing the desirability of giving binomials to recognized hybrids he suggested that such names rest upon a different basis from those of real species that are distinguished by constant morphological differences; and that since they must be applied to a variable group of plants having a common mixed parentage, they are merely a phase of nomenclature rather than of taxonomy. Some of the difficulties of using the first method were shown and examples were given of the complications that arise when a new name is taken up for one or both of the parent species. A list of the hybrid binomials previously published was given in this paper and 25 new ones were proposed. Type specimens were designated and brief descriptions accompanied by plates were given for two of the newly named hybrids. These were \times *Quercus paleolithicola* and \times *Q. Schuettei*. For the other hybrids only the supposed parentage was given, except for brief explanatory notes on a few of them.

A second and fuller treatment of the recognized hybrids was incorporated by Trelease in his monographic work, *The American oaks*, published in 1925. In that work 55 hybrids were named, six of them under new binomials, and another, \times *Quercus Byersii*, was credited to Sudworth in lit. Several previously published names were treated as synonyms. Brief descriptions were given of the newly recognized hybrids as well as of some of those named in the earlier publication, and bibliographical references were supplied for all of them.

Although most of Trelease's monograph was devoted to descriptions of the oaks of Mexico, it is a curious and perhaps a significant fact that no hybrids were recognized in that region. Fuller evidence will in all probability show that they are at least as abundant relatively south of the Rio Grande as in the United States, and it is not unlikely that a number of species recently described from Mexico will prove to be of hybrid origin.

In the interval between the appearance of Trelease's two publications Professor C. S. Sargent contributed a paper (53) in which 11 new hybrids were named and described and a variety was proposed for one of those named by Trelease, (\times *Quercus subfalcata* var. *microcarpa*). Type specimens and other collections were cited by Sargent for his newly proposed

hybrids. A description was also given of \times *Quercus Millechampii* Trelease, and an amplified description of \times *Q. dubia* Ashe. The latter was held to be a cross between *Quercus cinerea* and *Q. laurifolia*, and \times *Q. atlantica* Ashe and \times *Q. sublaurifolia* Trelease were given as synonyms.

Several new hybrids have been named and described since the publication of the papers by Trelease and Sargent, and a number of references to hybrids or supposed hybrids among the oaks have appeared in botanical papers and plant lists without binomials having been proposed for them.

A large amount of material of known or suspected oak hybrids has been brought together in the herbarium of the Arnold Arboretum and many of the hybrids have been grown here both from grafts and from seeds taken from the native trees. This paper is based largely on a study of the herbarium and living material in the Arboretum and on observations and notes made on native trees in many parts of the United States. A few specimens have also been examined in the Gray Herbarium and in the herbarium of the New England Botanical Club. Only a beginning has as yet been made in the study of oak hybrids, and much more field work and experimental work will be necessary before many doubtful questions can be resolved. Some hybrids are so well authenticated by ample material and by the obvious intermediate characters of the plants that there can be little or no reasonable doubt as to their identity. Other identifications must be regarded as merely hypothetical, and in some cases it is very doubtful whether the parentage that has been imputed to them is the correct one or whether they are really hybrids. Some cases of doubtful identity are discussed in this paper after an examination of the material and evidence available, but it is not possible to decide definitely on all of them. But since hybrids are likely to be found in our native woods wherever two or more species of oak of the same section or subgenus grow together, and since they are a source of perplexity to most students, it may serve a useful purpose to bring together a list of those that have been named or that can be recognized with some degree of certainty, and to review briefly the evidence on the subject.

The doubts entertained by the early botanists as to the occurrence of "spontaneous mixed races in nature," as expressed by Nuttall, are understandable when the views generally held at that time as to the origin and nature of species are taken into account. But in view of the accumulating evidence, it is scarcely to be believed that any competent observer would today question the existence of natural plant hybrids or that he could fail to find examples of them in the field, if he keep his eyes open. Hybrids among the oaks are probably much commoner than they were believed to be by most botanists even a few decades ago, and it seems probable that most if not all of the species within the sections of the annual-fruited (*Leucobalani*) and the biennial-fruited (*Erythrobalani*) are inter-fertile under the right conditions. But while this is true, it must not be inferred that individual trees of hybrid origin are relatively abundant in nature. A keen observer with a general knowledge of the native species is likely

to find hybrids by careful searching in any region where compatible species grow in close proximity; but he will probably encounter hundreds of thousands or even millions of trees of the different species for every hybrid. It is more than thirty years since the writer became interested in hybrid oaks, and for many years he has been on the outlook for them while collecting in many parts of the United States. It is perhaps not claiming too much to say that a certain skill and understanding of the problem has been developed. But in all this time and over so wide a territory probably not more than a few hundred trees of unquestionable hybrid origin have been encountered.

The greatest care and caution are necessary in studying hybrid oaks both in the field and in the herbarium. Observations and field notes on the compatible species growing in the vicinity of the supposed hybrid are most important in determining the parentage, and this often limits the possibilities very narrowly. There is no way of determining definitely which parent species was the sire and which the mother tree, although, as will be shown later, it may in some cases be inferred with considerable probability. It is the conventional practice to write the names of the supposed parents of a natural hybrid in alphabetical order, as *Quercus alba* \times *bicolor*, and not the reverse.

It must not be assumed that all aberrant forms are to be explained as hybrids. Adventitious shoots, sterile branches and juvenile growth often produce leaves of abnormal types or texture in many of the oaks. Sometimes after a period of drought followed by abundant rain trees will put out new growth with leaves very different from the normal ones of the species. The same thing may happen if the tree is defoliated by insects and a second growth of leaves develops. In some cases these and other monstrous forms of leaves have some resemblance to the leaves of hybrids, and the uncautious or inexperienced student is likely to be deceived by them. Without full material and a careful study of the living plants the identification of spontaneous hybrids can sometimes be only tentative and hypothetical. The fact of hybrid origin and the parentage of the cross must be inferred from certain stigmata and from the intermediate character of the leaves, fruit and other parts of the plant. In a hybrid these marks run through the entire plant and are not confined to certain shoots or branches, as is often the case in abnormal growth resulting from injury or arrested growth, and they differ also in character from monstrous forms, in which the leaves of entire plants sometimes become flabellate, laciniate, crisped or otherwise distorted.

It may be assumed that the ideal hybrid of the first generation would be exactly intermediate in characters between the parent species, but it is quite unlikely that any such perfectly balanced individual could be found in nature. There is wide variability in different parts within every species of oak, as in most other plants, and in a hybrid the different, variable characters of the parents may be combined in various ways or any of them may be predominant or subordinate in different degrees. Latent char-

acters or tendencies in the parent species may also be brought out or may be accentuated. Examples of this may be seen in the extremely large winter-buds of some hybrids, in strange and exaggerated leaf patterns and in an accelerated rate of growth.

The most obvious and easily detected hybrids are those between species in which the leaves are narrow and nearly or quite entire, as in the willow-oak, shingle-oak, laurel-oak or live oak, and species with broad and deeply cut leaves. Hybrids of this character were the first to attract attention, and their parentage can sometimes be determined from the leaves alone or with the aid of field observation. The leaves of such hybrids are generally extremely variable in outline and they are often bilaterally asymmetrical. Some of them may be unlobed, as in the entire-leaved parent species; in others the margins may be irregularly undulate, or there may be one or more rounded or sharp pointed lobes on one side or on both sides of the blade. In rare cases the lobes on vigorous shoots may be prolonged or exaggerated beyond anything found in the parent species. It is as if the growing plant had become bewildered between the two leaf-patterns and the cells did not know which direction to take or how to arrange themselves.

In some hybrids in the white oak section, such as those between the chestnut-oaks and species with deeply cut leaves, symmetry of outline is usually preserved but the lobes are almost always simple and intermediate in length between those of the parents. In many species of *Quercus* the fruit is less variable and is of greater diagnostic value than the leaves. This is equally true in hybrids, and in many cases mature acorns should be seen before definite conclusions are reached as to the parentage. Unfortunately, many hybrid oaks are without fruit, either because they are found as juvenile plants or because of a real tendency to sterility. The latter may be true in some cases, but some hybrid trees produce fruit in great abundance. Hybrids between species in which the acorns differ greatly in size, shape or character of the cup-scales can usually be detected by the intermediate type of fruit; winter-buds and bark may furnish valuable clues, and these are particularly valuable in identifying hybrids between species with similar leaves. In general it may be said that the facility and certainty with which any natural hybrid can be identified is in inverse ratio to the similarity of the parent species.

Among common American oaks there are a number of closely related and similar forms, most of which have been treated as distinct species by some authors and as subspecies, varieties or forms by others. Some examples are *Quercus borealis* and *Q. maxima*; *Q. Shumardii*, *Q. texana* and *Q. Schneckii*; *Q. falcata* and *Q. pagoda*; *Q. laurifolia* and *Q. obtusa*; *Q. virginiana*, *Q. minima* and *Q. geminata*; *Q. macrocarpa* and *Q. mandanensis*; *Q. Muhlenbergii* and *Q. prinoides*; *Q. stellata* and *Q. Margaretta*; and *Q. Durandii*, *Q. breviloba* and *Q. austrina*. A number of others are found in the western and southwestern states. Whatever status is given to such closely related oaks, it may be assumed that hybrids would be at least as likely to arise among them where the different pairs or groups grow in

proximity as between more distantly related species. But in most cases it would be extremely difficult or impossible to recognize or to identify such hybrids on morphological evidence. It is not unlikely that some of the slightly atypical forms that occasionally turn up to confound students and authorities may have originated from such crosses.

Sargent in his description of \times *Quercus Harbisonii* gave the parentage as *Q. stellata* var. *Margareta* \times *virginiana* var. *geminata*, and this according to Trelease is *Q. geminata* \times *Margareta*. But plants that appear to be hybrids between the typical forms of *Quercus stellata* and *Q. virginiana* have been found in several places and an artificial hybrid between the species was produced by Ness. The type specimen of \times *Quercus Harbisonii* was labeled *Q. minor (stellata)* \times *virginiana* by the collector, and I can see no convincing evidence in the specimen that it was not a cross between the typical forms of the two species, nor that it differs in any important character from the other specimens believed to be crosses between the post-oak and the live oak. The supposed parentage of \times *Quercus pseudomargareta* was given by Trelease as *Q. Margareta* \times *stellata*. According to Sargent *Q. Margareta* is a variety of *Q. stellata*; so in this case we would have, if we follow Sargent, a cross between two varieties of the same species. But even if the two are held to be distinct species, they are so similar in foliage, fruit and other characters and are so closely connected by intermediate forms that recognizing a hybrid between them would seem to require some faith and imagination. A similar situation exists with reference to other hybrids in which one of the supposed parents is of debatable specific or varietal rank. *Quercus Shumardii* var. *Schneckii* was named as one of the parents of \times *Quercus Shirlingii* Bush and of \times *Q. mutabilis* Palmer & Steyermark, but except on grounds of propinquity, it would have seemed just as probable that the typical form of *Q. Shumardii* was involved. If *Quercus borealis* and *Q. maxima* are regarded as distinct species, it becomes a question which of them was one of the parents in such hybrids as \times *Quercus heterophylla*, \times *Q. Hawkinsii*, and others. According to Trelease, \times *Q. heterophylla* is a cross between *Q. maxima* and *Q. Phellos*. If this is accepted and *Q. borealis* is held to be a distinct species, a cross between it and *Q. Phellos* would be another hybrid and should receive another name. It is not unlikely that both forms of the northern red oak may have hybridized with the willow-oak or with other species at times, but it is scarcely possible that any marked differences between them could be found or recognized in spontaneous plants.

The question of varieties of a named hybrid also arises. Can or should forms or varieties of the hybrid "species" be recognized and named? Sargent, as mentioned above, proposed a variety of \times *Quercus subfalcata*, and Baenitz in his description of \times *Q. Benderi* subdivided it into the variety *coccinoides*, with a forma *voluto-annulata*, and variety *rubroides*, indicating which parent species the hybrid resembled more closely. Such subdivisions might be multiplied indefinitely, since it must be expected

that hybrids of identical parentage will be widely variable. To attempt to give distinct botanical names to all such forms would, in my opinion, result in complications that would more than offset any advantages. But in the case of plants of particular ornamental or economic value and of distinct appearance, it might be worth while to give them horticultural names.

Only a single tree of \times *Quercus heterophylla* and of \times *Q. Leana* had been discovered when they were described, and while a number of examples of both of them have since been found, they are both comparatively rare as wild plants. This is true of all hybrids, and it affords some aid in detecting and distinguishing them. But the fact that a form of oak is rare or unique in a locality does not prove it to be a hybrid though it may strongly suggest it; for real species are seldom found so isolated unless the tree is beyond its general range, and in that case it will usually be known to be abundant elsewhere.

Hybrids are most likely to occur in nature along the margins of the range of one of the parent species or where one is locally rare and the other abundant. The reason for this is rather obvious; the chance of the rare plant being pollinated by one of its own kind is small or nonexistent, except in so far as it may be effected by self-pollination. On the other hand, the chance of its pistillate flowers being fertilized by the wind-borne pollen of the dominant species is very great. In the case of a hybrid found under such circumstances it may almost be assumed that the rare species was the mother plant.

It may be stated as a general principle that, other factors being equal, the chance for the production of natural hybrids between compatible species increases in proportion to the numerical inequality of the parent species in the immediate vicinity. Another significant implication of this fact is that in hypothesizing the parentage of a hybrid, especially if it is an old tree, it is not absolutely essential that both species be found growing with it, providing they are natives of the region and are known at no great distance. For if one of the parents was a lone individual it may well have disappeared from the locality.

While collecting in southern Illinois in 1919 and 1920 my attention was first called to this principle as applied to hybrid oaks. The willow-oak (*Quercus Phellos*) barely enters the state from the south near the junction of the Ohio and Mississippi Rivers. A few scattered specimens were found in Alexander, Massac, and Pulaski counties in a region where the pin-oak (*Quercus palustris*) is a common and dominant species. In almost every locality where there was a single large willow-oak — and in some where none was seen — obvious hybrids between this species and the pin-oak were found. Some of the hybrid plants were mere sprouts that probably would not long survive, but several had attained considerable size. Similar evidence has been obtained in regard to other hybrids at different localities. Specimens of \times *Quercus Leana* are often found along the border of the range of the shingle-oak, and of \times *Q. Saullei* where *Q.*

alba is locally dominant and *Q. montana* rare. In the localities where $\times Q. bimundorum$, described in this paper, has appeared the white oak is a common tree and the English oak is known in cultivation in the vicinity, or it may rarely be found as an escape. Obviously, natural hybrids may arise where the parent species are more evenly balanced in numbers, but the chances for them are relatively less.

As may be seen by looking over the literature listed in the bibliography at the end of this paper, most of it deals with accounts and descriptions of hybrids found in nature and with discussions of them. Only a small amount of work has been undertaken so far for the purpose of testing supposed hybrids by growing seedlings on a large scale under experimental conditions, and still less has been done in the controlled production of oak hybrids by cross-pollination.

MacDougall (34) mentioned the generally unreliable and hypothetical character of the evidence as to supposed hybrids in nature and he thought that they should be regarded merely as suggestions to be tested by cultural and experimental methods. He suggested three possible lines of attack on the problem of the hybrid; (1) by synthetizing it from its supposed parents; (2) by making an anatomical examination of the hybrid and the supposed parents; (3) by growing the plants to see whether there will be a separation of the ancestral characters in succeeding generations and a reversion of some plants to the parent species. At the same time he pointed out some of the difficulties and uncertainties as to the results that attend such experiments. Cross-pollination in nature may have taken place under an exceptionally favorable combination of circumstances that can scarcely be reproduced artificially. One or both parent species as ordinarily recognized may in reality have consisted of two or more elementary species which might give quite diverse results in breeding. The characters of the hybrid offspring might be quite different if the roles of the parent species, as to which was the sire and which the mother plant were reversed, as was indicated by experiments with *Oenothera*. After growing a number of seedlings from acorns collected from native trees of $\times Q. heterophylla$ and $\times Q. Rudkini$, he concluded that the former was without doubt a hybrid between the willow-oak and the northern red oak, but that the evidence was inconclusive as to the hybrid character of $\times Q. Rudkini$.

Allard (3) gave an account of seedlings grown from several individuals of $\times Q. Saulei$ found in the vicinity of Washington, D. C. About 40 seedlings were grown by him, some of which had attained a height of 15 feet in ten years. The leaves showed considerable variation in outline, with a dominance of *Q. montana* characters in the comparatively shallow, more numerous and uniform lobes and in the presence of more or less whitish pubescence beneath. However, a few individual leaves showed the *Q. alba* influence in the larger, irregular lobes. Different individuals also showed variation in autumn coloring, a number of them assuming the typical red-brown color of the *Q. montana* parent, and others the coppery red of *Q. alba*, while one individual with an obviously *Q. alba* type of

leaves became brilliantly deep-red. In some of the plants the leaves showed a tendency to cling to the branches until late in the season, as in *Q. alba*, while in others they resembled the *Q. montana* parent in being early deciduous. In Allard's paper several other hybrid oaks or supposed hybrids were reported as growing in the vicinity of Washington, and the leaves, fruit, and winter-buds of some of them were figured. One of the most interesting of these was the cross between *Quercus palustris* and *Q. Phellos*, of which two trees were said to be growing in a planting of willow-oaks on Pershing Drive, just east of Glebe Road. The experiments and publications of Gale, MacDougall, and others on hybrid oaks were mentioned, the need for further study and experimental work was suggested.

In 1909 Professor Helge Ness began experiments in the cross-pollination of oaks at the Texas Agricultural Experiment Station, College Station, Texas, and obtained some significant results. The most striking of these was a cross between the overcup oak (*Quercus lyrata*), used as the sire, and the live oak (*Q. virginiana*), as the mother plant. This hybrid has also been found growing spontaneously in several places, and was named \times *Quercus Comptonae* by Sargent.

Ness published a brief account of this hybrid in 1918 (39), and a second paper with a fuller account of work on hybrid oaks appeared in 1937 (40). At the time of the first report four of the hybrid trees planted on the College campus had produced acorns although there had been no male flowers, and the pollen for the fertilization of the female flowers must have come from other trees, probably post-oak (*Quercus stellata*) growing in the vicinity. The hybrids were symmetrical trees of rapid growth and with attractive foliage, intermediate in character between the parent species but with the overcup predominant.

In the second paper it was reported that seven trees of the original cross-pollination had grown to full fruiting size and all of them had within the preceding two years produced a profusion of both male and female flowers, and while six of them had matured crops of acorns, the seventh had remained sterile. The leaves of the second generation plants grown from these acorns showed wide variability ranging from forms quite intermediate between those of the overcup oak and live oak to others that could scarcely be distinguished from one or other of the parents. Mention was also made of plantings of live oaks on the college grounds where the trees began to bear female flowers about five years after they were set out but no male flowers until several years later. Yet the young trees so placed that they could scarcely receive pollen from any of their own species bore crops of acorns. Several hundred seedlings were grown from these, and the leaves ranged in character between those of the post-oak and live oak, with forms that resembled neither. Ness also produced hybrids through artificial pollination between *Quercus stellata* and *Q. virginiana*, and between the latter and *Q. bicolor*, and he mentioned a tree in the same planting that had been grown from seed of a white oak growing beside a post-oak, and that was an evident hybrid of the two species.

S. H. Yarnell (72), and W. S. Flory, Jr. and F. R. Brison (25) have more recently published papers on the Ness hybrids and have added valuable additional information about them. A brief paper by Ernest J. Schreiner and John W. Duffield (56) mentions an artificial cross having been made between the white oak (*Quercus alba*) and the English oak (*Q. robur*). Spontaneous hybrids between these species have also been found and are described later in this paper as \times *Quercus bimundorum*.

While attempts have been made over a number of years to bring as many as possible of the hybrid oaks into cultivation at the Arnold Arboretum, no experimental work has so far been carried on in growing seedlings in quantity under test conditions for scientific study. In some cases a number of seedlings were grown from seeds taken from spontaneous hybrids or from other cultivated trees, but usually only a few specimen plants were selected from them. Other hybrids were propagated by grafts or by transplanting rooted plants. The conclusions that can be drawn from the collection are, therefore, limited but not without interest.

Records show the following hybrids to be in cultivation at the Arboretum or to have been grown here at some time in the past. Several of those on the list did not live long enough to produce fruit or to be of much value for study and, unfortunately, the records of some of the introductions have been lost and other plants have been destroyed or injured by fires or other causes. Those of which specimens were still growing in the collection in 1946 are marked with an asterisk (*); those grown from seed are indicated by S, grafts by G, and where received as rooted plants by P. In a few cases there is no record.

\times *Quercus Bebbiana** S, G, P.

- " Bushii
- " Comptonae* S.
- " Deami* S, P.
- " exacta* S, G, P.
- " Fernowi S.
- " filialis* S.
- " garlandensis S, G
- " Hastingsii G.
- " Hawkinsi* S.
- " heterophylla*, G. P.
- " Hillii*, S, G
- " humidicola S, G.
- " Jackiana* S, G.
- " Leana* S, G.
- " ludoviciana

var. *microphylla* P.

\times *Quercus macnabiana* S.

- " mutabilis S.
- " mutabilis S.
- " Rehderi* S, P.
- " Robbinsii G.
- " Rudkini* S.
- " runcinata* S, G.
- " Sargentii* S, G.
- " Saulei* S, G, P.
- " Schockiana G.
- " stelloides S, G.
- " vaga
- " Walteriana S.
- " bicolor \times *montana*(?) S, G.
- " aliena var. *acutissima*
- \times *alba** (?) P.

Most plants that have been grown at the Arboretum from seeds of the original hybrids found in nature and a few second generation plants from cultivated trees have reproduced the characters of the hybrid parent more or less closely, and in some cases with remarkable fidelity. There seem to be a few exceptions to this, and it is a question whether other aberrant forms or reversions may not have been discarded in selecting plants for the collection. Only in a few cases were enough seedlings kept to afford a basis for comparison.

\times *Quercus Comptonae* was grown from seeds sent by Miss Compton from Natchez, Miss. in 1932, and nine plants were set out, of which four or five were living recently. They made slow growth and none of them attained much size, so only the leaves could be studied. These all showed unmistakably the intermediate character of the hybrid with considerable diversity in each individual and slight average variation in width and lobing on the different plants. It is interesting to find that this hybrid offspring of two southern species is hardy in the Arboretum, as the live oak has never survived the New England winters, although the overcup oak has been successfully grown.

\times *Quercus Leana* has been grown from seeds from several sources, and the seedlings kept are all examples of this hybrid though with some variations in foliage and fruit. Five plants of one lot from seed collected in southern Illinois were set out, and two of them have produced fruit. The leaves of the different individuals differ considerably in average size and outline. Most of them show some undulation or traces of irregularity or lobing on some of the leaves. But in two of the plants nearly all of the blades are entire and resemble some broad-leaved forms of the shingle-oak. On the other extreme is one tree in which the leaves are nearly all irregularly lobed or undulate. The acorns are intermediate in character between those of the parent species.

Six plants of a culture of \times *Quercus Rudkini*, from seeds of a tree found near Fulton, Arkansas, were set out and the leaves were studied before some of them were damaged or destroyed by fire. In all but one of the plants the leaves are mostly narrowly lanceolate and entire, somewhat resembling those of the willow-oak, though somewhat larger and broader than is usual in that species. But they are thicker in texture, strongly veined and pubescent when young on the under side and are sessile or nearly so and often rounded or slightly subcordate at base, all characters indicating the influence of the black jack oak (*Quercus marilandica*). One tree of the lot had much broader, more irregular and mostly lobed leaves. A tree of \times *Quercus runcinata* grown from seed of a tree found in southern Illinois in 1919, has made a remarkably rapid growth and in 1945 it was about forty feet in height with a trunk diameter of about fourteen inches. The leaves are broader and more uniform in shape than those of the parent tree and there is some resemblance to a narrow-leaved form of *Quercus borealis*. But some leaves show a tendency toward eccentric lobing and they are covered with a coat of easily-detached pubescence on the under side while young. The acorns, of which there was a large crop in 1945, are somewhat similar in size and shape to those of *Q. borealis*, but with loose scales on the cups suggestive of the *Q. imbricaria* parent. The two large trees of \times *Quercus Sargentii*, from seed of the hybrid tree first recognized in cultivation, both show unmistakably the characters of *Q. montana* and *Q. robur*, although differing noticeably from each other in foliage and fruit. Of three lots of \times *Quercus Deamii* from seeds of the original tree none resemble the parent

very closely and in the leaves of two of them there is a strong suggestion of *Quercus bicolor*. None has yet produced fruit.

It has been stated that most or all of the species within the two main sections of white oaks and black oaks are interfertile and that in some cases at least they produce viable fruit in abundance. There is also evidence that some of them reproduce themselves with little change, retaining characters intermediate between the parent species. Since several species are often found growing together in the deciduous forests throughout North America, it may be asked, as Englemann asked, why are hybrids not more common and why do they not tend to spread in their native woods and to become dominant in some areas?

Perhaps there are physiological reasons that tend to reduce the fertility of some oak hybrids, but evidence is lacking on this. And without resorting to such an explanation, probably a sufficient answer can be found in the keen competition for survival and reproduction among plants in nature. In a well occupied forest there is little chance for expansion, and reproduction is held to a minimum except where the pressure is relieved by some extraordinary chance or vicissitude, such as an artificial clearing or thinning or a similar result brought about by such natural causes as fire, hurricane, climatic extremes, or disease among some of the competing species. A large oak tree living for perhaps a century or more may produce literally millions of acorns. But in spite of this almost incredible fecundity, very few of them will ordinarily find a chance to germinate and of the seedlings that do spring up perhaps only one or at best only a very small number is likely to survive and to replace the parent as a fully grown tree. Even under the most favorable conditions for hybridization the chance of the fortunate survivor having sprung from an acorn produced by cross-pollination would seem to be extremely small.

In a hybrid found in nature there is of course no way of determining whether it is a cross of the first or of a later generation. But the probability seems to be very great that it is the first. For if the chance for the development and survival of the original hybrid are so small, the odds against its perpetuation in a second generation are infinitely greater. It has been suggested that certain supposed hybrids found in nature represent crosses between more than two species, or in other words, that the bispecific cross has been recrossed with a third species. The isolated hybrid produced by the fertilization of a rare or single mother plant by another and locally common species would in all probability be pollinated by the dominant species. And so in the improbable case of succeeding generations there would be an increasing tendency to revert to the characters of the male parent. It may be possible that under a combination of particularly favorable circumstances a hybrid might be pollinated by a third species and a compound hybrid result. But the chances for it occurring in nature seem so remote as to be almost negligible. It seems probable, therefore, that the great majority of natural hybrids are first-generation crosses between two species.

Several instances of experiments and results in the artificial production of oak hybrids have been referred to above. But comparatively little has so far been done in this field, although it would seem to be a most promising one both from the standpoint of its practical value and its scientific interest.

In several cases the specific names used for one or both of the parent species in the original publication of hybrid binomials have been changed to conform to more recent usage or interpretation. Among examples are *Quercus nigra* L., long used for the black jack oak but now held to apply properly to the water-oak of the southern states, *Quercus falcata* Michx., which has again been taken up for the southern red oak instead of the doubtful *Quercus rubra* L., *Quercus Prinus* L., now used for the basket-oak of the southern coastal plain instead of for the rock-chestnut-oak, which is now called *Quercus montana* Willd., and a number of others. The names originally used are generally shown in parentheses or are explained in the descriptions. Differences of opinion as to the proper use of certain names and in regard to the status of some named species, varieties, and forms still exist among botanical authors. The names currently accepted as valid in the herbarium of the Arnold Arboretum are used in this paper.

The figures in parentheses refer to the numbers of papers listed in the bibliography. Specimens cited that were examined only in the Gray Herbarium are designated by (G); all others are in the herbarium of the Arnold Arboretum.

× *Quercus anceps* hybr. nov. (*Q. falcata* × *imbricaria*).

Arbor foliis obovatis vel oblongo-ellipticis undulatis vel inaequaliter lobatis 9–16 cm. longis 4–10 cm. latis apice acutis mucronatis basi cuneatis vel anguste rotundatis, maturis supra glabris infra fulvo-tomentosis. Fructus ignotus.

The trees from which the type of this hybrid came were found along the margin of upland woods near Rosiclair, Illinois, with both of the supposed parent species growing near by. Other biennially-fruited oaks in the vicinity were *Quercus borealis* var. *maxima*, *Q. marilandica*, and *Q. velutina*. Unfortunately, there were no acorns either on this tree or on another of apparently similar parentage found near Shawneetown, Ill. But the shape, texture and color of the leaves and other characters furnish convincing evidence of the parentage. The narrowly obovate or oblong-elliptic leaves are remarkably variable and many of them are asymmetric in outline. The range of the shingle-oak and of the southern red oak overlap in only a few localities, and the latter was near its northern limit in the locality where the hybrid was found.

ILLINOIS: Rosiclair, Hardin Co., E. J. Palmer 15455, June 10. 17031 (TYPE), Oct. 10, 1919; Shawneetown, Gallatin Co., E. J. Palmer 15560, June 19, 1919.

× *Quercus Andrewseii* Sargent (*Q. macrocarpa* × *undulata*), Bot. Gaz. 65: 455. 1918.
— Trelease, Mem. Nat. Acad. Sci. 30: 13. 1924.

This was described from a specimen taken from a group of large shrubs spreading by underground stems, found in Dewey County, western Oklahoma. Both of the supposed parents were growing near by. The

leaves are intermediate in size and shape between those of the parent species, the pubescence on the under surface being very much like that of *Quercus macrocarpa*. The single acorn on the type specimen is about 2.5 cm. long including the rounded or slightly turbinate cup which covers nearly half of the nut; cup scales pale pubescent, corky thickened toward base, the tips on upper rows prolonged and forming a short, sparse fringe along the rim.

OKLAHOMA: Seibring, *D. M. Andrews* 69 (TYPE), Aug. 17, 1915.

Although known from only a single collection, there can be little doubt as to the hybrid origin and parentage of this plant.

× *Quercus Asheana* Little (*Q. incana* × *laevis*), *Jour. Washington Acad. Sci.* 33: 8. 1943.

× *Quercus Ashei* Trelease (*nomen nudum*), *Proc. Amer. Phil. Soc.* 56: 48. 1917; *Mem. Nat. Acad. Sci.* 20: 13. 1924. Not *Q. Ashei* Sterrett, *Jour. Elisha Mitchell Sci. Soc.* 37: 178. 1922.

Quercus cinerea × *Catesbaei* Ashe, *Jour. Elisha Mitchell Sci. Soc.* 11: 88. 1894.— Small, *Bull. Torrey Bot. Club* 22: 76, pl. 234–235. 1895.

Quercus brevifolia × *Catesbaei* Sudworth, *U. S. Dept. Agric., Div. Forestry, Bull.* 14: 170. 1897.

Although no description of this hybrid was given by Trelease, the name and the reference to Ashe's report clearly indicate the source. Two forms were described by Ashe: (1) having the bark and general appearance of *Q. cinerea* (*incana*) but with twigs, buds and fruit somewhat resembling the other parent, and (2) with the general appearance of *Q. Catesbaei* (*laevis*), but with acorns generally like those of *Q. incana*. It was stated that ten or twelve of the first form were seen and several of the latter, but no definite locality was mentioned. The following specimens of this hybrid have been seen:

GEORGIA: Traders Hill, *J. K. Small*, June 12–15, 1895; St. Marys, *J. K. Small*, June 13, 1895; Folkstone, *T. G. Harbison* 50, May 15, 1918, 106, Nov. 26, 1919.

FLORIDA: Ella, Lake Co., *Geo. V. Nash* 1577, Aug. 1894; Umatilla, Lake Co., *Geo. V. Nash* 1586, Aug., 1894; Zellwood, Orange Co., *C. H. Baker* 491-a-b-c-d-e, April 16, 1918; Orlando, Orange Co., *T. G. Harbison* 23, Dec. 5, 1917, *E. J. Palmer* 38433, April 2, 1931; Jacksonville, *T. G. Harbison* 1, 6, Nov. 9, 29, April 23, 1917; Gainesville, *T. G. Harbison* 54, Nov. 11, 1917, 70, July 25, 1918; Sebring, *T. G. Harbison* 41, July 29, 63, July 30, 1918; Haines City, *T. G. Harbison* 4, Aug. 1, 1918; Lakeland, *T. G. Harbison* 4, 13, Aug. 1, 1918; Brookville, Hernando Co., *J. Kelley* 21, Sept., 1941. MISSISSIPPI: Biloxi, *T. G. Harbison* 16, May 6, 1918.

× *Quercus atlantica* Ashe (*Q. incana* × *obtusa*?), *Proc. Soc. Amer. Foresters* 11: 88. 1916.— Trelease, *Mem. Nat. Acad. Sci.* 20: 13. 1924.

× *Quercus dubia* Sargent, *Bot. Gaz.* 65: 452. 1918, in part, not Ashe.

Ashe described this as a new species but with the note that, "This tree might be considered a hybrid between *Quercus cinerea* and *Q. laurifolia*, but for the fact that both the fruit and the foliage are larger than in either of those species." But a careful reading of the description and an examination of Ashe's specimens from the type locality and other stations suggest that it is probably a cross between *Quercus incana* and *Q. obtusa*. All three species are found near the type locality. *Quercus obtusa* and *Q. laurifolia* are closely related and very similar species and it is not always

easy to distinguish between them. The same difficulty may be found in trying to identify hybrids in which they are involved, such as \times *Quercus atlantica* and \times *Q. sublaurifolia* discussed later. The best distinguishing characters between the species are that in *Quercus obtusa* the leaves are slightly larger on the average, usually broadened above the middle, rounded or obtuse at the apex, thinner in texture and earlier deciduous than in the laurel-oak; the acorns are also larger.

GEORGIA: Lumber City (Telfair Co.), *W. W. Ashe* 10, 1915 (TOPOTYPE), *T. G. Harbison* 6, May 30 and Dec. 15, 10, 13, May 30, and 15, Dec. 16, 1917; Climax, *T. G. Harbison* 11, Nov. 6, 1917. FLORIDA: near Jacksonville, *A. H. Curtis* (without no. or date), *T. G. Harbison* 4, 5, Dec. 7, 2, 11, 12, Dec. 10, 23, Dec. 3, 1917; Zellwood, *T. G. Harbison* 3, Dec. 4, 1917; Lake City, *T. G. Harbison* 23, June 23, 1917; Gainesville, *T. G. Harbison* 160, 164, Dec. 4, 1917, 202, Sept. 18, 1919.

\times *Quercus Beadlei* Trelease¹ (*Q. alba* \times *Prinus*), Proc. Amer. Phil. Soc. 56: 48. 1917; Mem. Nat. Acad. Sci. 20: 13. 1924.—Sargent, Man. Trees N. Amer. ed. 2, 203. 1922.

Quercus alba \times *Michauxii* Britton and Shafer, N. Amer. Trees 203. 1908.

Although no description was given and no type specimen was cited by Trelease, this hybrid was, no doubt, based on a specimen in the Biltmore Herbarium, no. 5723b, May 10 and Oct. 13, 1897. The earlier collection consisted of young leaves and flowers to which mature leaves and acorns were added in autumn. There seems to be no reason for questioning the parentage. The leaves are intermediate in shape between those of the parent species, with 6–12 pairs of rather uniform deeply divided lobes. While young they are coated beneath with pale, loosely attached tomentum, and at maturity they often become nearly glabrous except for tufts of tomentum in the axils and along the principal veins. The acorns of the type specimen and of most of the other fruiting specimens I have seen resemble those of *Quercus alba* in size and in the coky thickening of the scales of the cups, but in a specimen from Jackson Co., Indiana, they are quite similar to those of *Q. Prinus*. In this and another Indiana specimen the mature leaves are unusually pubescent beneath.

NEW JERSEY: near Newtonville, Atlantic Co., *J. W. Adams* 4081, Sept. 24, 1937. DELAWARE: Kiawense Station, near Wilmington (without date or name of collector). VIRGINIA: south of Seatack, *M. L. Fernald & Bayard* Long 3902, July 30, 1934. NORTH CAROLINA: Biltmore, ex Herb. Biltmore, no. 5723b, May 10 and Oct. 13, 1897; swamps near Clarkton, Bladen Co., ex Herb. Biltmore, no. 5723c, June 25, 1897. FLORIDA: rich woods east of Tallahassie, *R. M. Harper*, Dec. 6, 1924. INDIANA: 3 miles east of Mendora, Jackson Co., *C. C. Deam* 19037, Sept. 13, 1915; near Bedford, *R. M. Kriebel*, 1934. TEXAS: near Cleveland, San Jacinto Co., *C. H. Muller* 3938, July 11, 1941.

\times *Quercus beaumontiana* Sargent (*Q. falcata* \times *obtusa*), Bot. Gaz. 65: 451. 1918, (as *Q. rhombica* \times *rubra*); Man. Trees N. Amer. ed. 2, 262. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 13. 1924, (as *Q. [laurifolia] rhombica* \times *rubra*).

The type specimen of this hybrid was collected from a tree growing in low, native woods, in close association with the supposed parent species,

¹ Arbor foliis obovatis vel oblongo-obovatis plerumque satis profunde 13–25-lobatis maturis supra glabris infra pubescentibus interdum solum ad venulas.

and not from a street tree as stated in the description. The intermediate character of the generally slightly asymmetrically lobed leaves suggest the parentage.

TEXAS: Beaumont, *C. S. Sargent*, April 11, 1915 (planted along street), *E. J. Palmer* 12748 (TYPE), Sept. 14, 1917, 13081, March 16, 1918; Sauer Lake, Hardin Co., *E. J. Palmer* 13109, March 18, 1918.

× *Quercus Bebbiana* Schneider (*Q. alba* × *macrocarpa*), Ill. Handb. Laubh. 1: 201. 1904.—Sargent, Man. Trees N. Amer. ed. 2, 302. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 13. 1924.

Quercus alba × *macrocarpa* Engelmann, Trans. Acad. Sci. St. Louis 3: 398. 1877.—Sargent, Silva 8: 18, pl. 360. 1894.

Specimens showing various degrees of transition between the parent species afford convincing evidence as to the hybrid origin and relationship of this plant.

CANADA: Ste. Anne de Bellevue, Que., *S. Baril*, Oct. 8, 1939. VERMONT: Charlotte, *C. G. Pringle*, Sept. 29, 1879. OHIO: Kenton, Hardin Co., *R. E. Horsey* 720, Sept. 27, 1918. INDIANA: Bedford, *R. M. Kriebel*, Oct. 1, 1932. MISSOURI: Hannibal, *J. Davis* 3629, Oct. 19, 1914; Swope Park (Kansas City), *B. F. Bush* 9313, 9314, Oct. 19, 1914, *E. J. Palmer* 22323, 22324, Oct. 21, 1922.

Also cultivated at the Arnold Arboretum and at Mt. Desert Nurseries, Bar. Harbor, Me. According to Schneider, this hybrid was first found by M. S. Bebb, near Fountaintdale, Ill., but I have not seen the specimen.

(?) × *Quercus Benderi* Baenitz (*Q. borealis* × *coccinea*), Allg. Bot. Zeit. 9: 84. 1903, (as *Q. coccinea rubra*).—Sargent, Man. Trees N. Amer. ed 2, 248. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 13. 1924.

Believed to have originated spontaneously in cultivation. The hybrid origin of the plant is indicated, according to Baenitz, not only by the intermediate morphological characters and the yellow color of the autumn foliage, but also by a microscopic examination of the stamens and by the fact that the acorns are often sterile. A hybrid between two such similar species as the northern red oak and the scarlet oak would, obviously, be obscure and difficult to distinguish. An examination of the specimens distributed by Dr. Baenitz rather suggests *Quercus ellipsoidalis* E. J. Hill, a tree that was scarcely known as a distinct species in Europe at the time × *Q. Benderi* was published, although it might very well have found its way into cultivation without having been recognized. The small acorns with the nut half or more enclosed in the narrow, turbinate cup are very similar to those of the jack oak, and the leaves of both forms come within the range of variability shown in that species.

Besides the specimens collected by Baenitz in Scheitniger Park, Breslau, Silesia, in 1902, showing a seedling and mature leaves and acorns of the varieties and form, I have seen others with nearly fully grown leaves, collected by C. K. Schneider from the original trees, May 24–28, 1904. There is also a sheet in the Arnold Arboretum herbarium collected by A. Rehder, Blue Hills, near Boston, Mass., Sept. 22, 1900, and doubtfully referred to this hybrid. The specimen is sterile and the leaves look much like those of *Quercus borealis*. Hybrids between *Quercus borealis* and

Q. coccinea are not unlikely to be found where the two species grow in proximity, but I am somewhat doubtful as to whether \times *Quercus Benderi* represents such a cross. It is perhaps best to leave the question open until fuller evidence is available.

\times *Quercus bernardensis* W. Wolf (*Q. montana* \times *stellata*), *Torreya* 18: 161. 1918.

Several trees of this apparent hybrid were found by Brother Wolf in the vicinity of Saint Bernard College, in Cullman County, northern Alabama, and they were believed by him to represent a new species. In the description he stated that *Quercus Prinus (montana)*, its principal associate, was confined to the rocky slopes and cliffs, while \times *Q. bernardensis* was found in a strip of lowland below the cliff. Other oaks mentioned as common in the vicinity were *Quercus alba*, *Q. stellata*, and *Q. velutina*. Trelease considered it a hybrid between *Quercus alba* and *Q. stellata* and therefore a synonym of \times *Q. Fernowi*. The leaves are clearly intermediate in shape between those of the chestnut-oak and the post-oak, and the acorn in the one specimen in which they have been seen also indicate this relationship.

DISTRICT OF COLUMBIA: near Rock Creek, ex U. S. Nat. Herb., May 9, 1884. ALABAMA: St. Bernard, Cullman Co., *W. Wolf A*, April 28, May 14, May 24, and Oct. 26, 1918, *B*, Sept. 14, 1918, *D*, May 14, 1918, *F*, June 4, 1918; Cullman Co., *T. G. Harbison 4, 6*, Nov. 3, 1919; Valleyhead, *T. G. Harbison 26*, June 26, 1918; between Maud and Trio, Bibb Co., *R. M. Harper*, June 11, 1924.

\times *Quercus bimundorum* hybr. nov. (*Q. alba* \times *robur*).

Arbor ad 10–12 m. alt., foliis obovatis, profunde incisis lobis 7–9 obtusis apice obtusis basi leviter contractis subcordatis vel auriculatis; petiolis 5–10 mm. longis. Fructus ovatus 1.5–2 cm. longus pedunculatus; squamis cupulæ rotundæ paulis crassis.

A small tree that is apparently a spontaneous hybrid between the white oak and the English oak was found by C. H. L. Gebfert on a wooded hillside on the west side of Centre Street, Jamaica Plain, Mass. This tree was fruiting abundantly. Two trees of the same hybrid were discovered by J. C. Swartley on the farm of Charles Mann, near Horsham, Pennsylvania, and a specimen of one of them with mature leaves and fruit was sent to the Arnold Arboretum. According to information furnished by Mr. Mann and transmitted by Mr. Swartley, the trees were grown from seeds collected from a tree near a farmhouse on an extension of the Easton Highway, not far from Ivy Hill Cemetery. A large English oak was also found near the road and both the white oak and swamp white oak were growing in the vicinity. The name Sydenham Oak was proposed by Mr. Mann for these trees, in honor of some of his family connections. Another specimen collected in 1917 from a tree growing in the Harvard Botanical Garden at Cambridge, Mass., appears to belong to the same hybrid.

MASSACHUSETTS: Jamaica Plain, *C. H. L. Gebfert*, Sept. 3, 1923 (TYPE); Cambridge, Botanical Garden (cult.), *J. G. Jack*, Sept. 13, 1917. PENNSYLVANIA: near Horsham, Montgomery Co. (cult.), *J. C. Swartley S-858*, Oct. 10, 1936.

Mention was also made in the introduction of the cross having been made artificially (56).

× *Quercus blufftonensis* Trelease (*Q. falcata* × *laevis*), Proc. Amer. Phil. Soc. 56: 48. 1917; Mem. Nat. Acad. Sci. 20: 14. 1924.—Sargent, Man. Trees N. Amer. ed. 2, 254, 1922.

The type of this is a sheet in the U. S. Nat. Herb., collected by J. H. Mellichamp at Bluffton, S. Car., Aug. and Oct., 1893. According to Trelease, it is very like × *Q. Mellichampi* except for its larger and thinner leaves. I have not seen the specimen nor any other material of this hybrid.

× *Quercus Brittoni* W. T. Davis (*Q. ilicifolia* × *marilandica*), Bull. Torrey Bot. Club 19: 301. 1892.—Sargent, Man. Trees N. Amer. ed. 2, 225. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 14. 1924.

Quercus nigra × *ilicifolia* W. T. Davis, Scientific American, Sept. 3, 1892; Proc. Nat. Sci. Assoc. Staten Isl., Sept. 10, 1892.

According to the author, a number of trees of this hybrid were found growing in sandy soil at Watchogue, on Staten Island, where both *Quercus ilicifolia* and *Q. marilandica* were abundant. Examination of material from the type locality and from several other stations furnishes convincing evidence of the validity of this hybrid.

NEW YORK: Watchogue, Staten Island, *W. T. Davis*, May 10 (and autumn), 1894. PENNSYLVANIA: Reading, Berks Co., *E. J. Palmer* 36321, Sept. 11, 1929; *David Berkheimer* 4412, Oct. 10, 1943. NEW JERSEY: Ocean Grove, *J. K. Hayward*, Sept., 1890.

(?) × *Quercus burnetensis* Little (*Q. macrocarpa* × *virginiana*), Jour. Washington Acad. Sci. 33: 9. 1943.

× *Quercus coloradensis* Ashe, Bull. Torrey Bot. Club 49: 268. 1922. Not Lesquereaux. 1888 (fossil).

The description of × *Quercus coloradensis* Ashe clearly indicates that the live oak is one of the parents, but there is little to suggest the bur-oak in any of the characters mentioned. I have not seen the type specimen nor any other material that can be referred to it. The type was collected along the Colorado River above Marble Falls, Texas.

× *Quercus Bushii* Sargent (*Q. marilandica* × *velutina*), Bot. Gaz. 65: 453. 1918; Man. Trees N. Amer. ed. 2, 259. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 14. 1924.

× *Quercus incomita* Palmer (as *Q. marilandica* × *rubra* [*falcata*]), Jour. Arnold Arb. 7: 120. 1926.

The type of × *Quercus Bushii* was collected near Sapulpa, Okla., and it has since been found at a number of other stations from Pennsylvania to South Carolina and westward to eastern Nebraska, eastern Kansas, and Mississippi. The intermediate characters of the leaves and fruit in the many specimens clearly indicate the parentage. In some specimens the young shoots are extremely vigorous and the winter-buds are larger than in either of the parent species. A further study of material from the type tree of × *Q. incomita* makes it seem probable that it may be of the same hybrid origin as × *Q. Bushii*, and it is accordingly treated as a synonym here.

PENNSYLVANIA: Reading, Berks Co., *E. J. Palmer* 36308, 36309, Sept. 11, 1929; *David Berkheimer* 4365, Sept. 25, 1943, 5700, Sept. 18, 1944. MARYLAND: near Lenham, Prince George Co., *W. R. Maxon* 6009, Aug. 31, 1914; 2 miles north of Harrisonville, Baltimore Co., *C. H. Muller* 4963, 4965, 4966, Oct. 12, 1941. NORTH

CAROLINA: Durham, *D. S. Correll* 6896a, Oct. 8, 1936. SOUTH CAROLINA: Spartansburg, ex Herb. Biltmore, no. 5723e, Oct. 5, 1897. GEORGIA: Climax, *T. G. Harbison* 7, Nov. 6, 1917; Danielsville, Madison Co., *K. M. Wiegand & W. E. Manning* 1045, Aug. 18, 1921. NEBRASKA: Table Rock, Pawnee Co., *Thos. Howe*, Sept. 25, 1920. IOWA: Soap Creek, Davis Co., *Ada Hayden* 9836, June 26, 1939. INDIANA: Decker, Knox Co., *C. C. Deam* 54322, Aug. 19, 1933, 54689, Oct. 8, 1933, *R. M. Tryon* 4262, Sept. 3, 1939. ILLINOIS: southwest of Elbow, Richland Co., *Robt. Ridgway* 3067, July 22, 1928. TENNESSEE: Roan Co., *D. M. Coffman*, Oct. 3, 1889. MISSOURI: Buckner, *B. F. Bush* 9706, Oct. 3, 1921, *E. J. Palmer* 22335, Oct. 22, 1922; Holmes Park (Kansas City), *B. F. Bush* 10368, Oct. 22, 1924; Allenton, *G. W. Letterman*, July 28, 1911; Pertle Springs, Warrensburg, *E. J. Palmer* 36747, June 23, 1930; Prosperity, Jasper Co., *E. J. Palmer* 15852, Aug. 15, 1919; Joplin, Jasper Co., *E. J. Palmer* 22735, May 21, 1923. ARKANSAS: Eureka Springs, *E. J. Palmer* 20509, Sept. 17, 1921; Fayetteville, *E. J. Palmer* 23950, Oct. 1, 1923. KANSAS: Neodesha, Wilson Co., *E. J. Palmer* 21379, May 23, 1922. OKLAHOMA: Sapulpa, *B. F. Bush* 1328 (TYPE), Sept. 20, 1895. MISSISSIPPI: Oxford, *T. G. Harbison* 16, Oct. 16, 1915.

× *Quercus Byersi* Sudworth ex Trelease (*Q. macrocarpa* × *Prinus*), *Mem. Nat. Acad. Sci.* 20: 14. 1924.

Quercus Michauxii × *macrocarpa* Sudworth, *U. S. Dept. Agric., Div. Forestry, Bull.* 14: 158. 1897.

The type was found near Covington, Tipton Co., Tennessee, associated with the bur-oak and the basket-oak, both of which are species of low or alluvial woods. I have not seen any specimens of this hybrid, but from the description and notes given by Sudworth there seems to be no reason to question the parentage.

× *Quercus caduca* Trelease (*Q. incana* × *nigra*), *Proc. Amer. Phil. Soc.* 56: 48. 1917; *Mem. Nat. Acad. Sci.* 20: 14. 1924.—Sargent, *Man. Trees N. Amer.* ed. 2, 266. 1922.

Quercus cinerea × *aquatica* Ashe, *Jour. Elisha Mitchell Sci. Soc.* 11: 90. 1894.

Ashe stated that several trees of this hybrid were found, all near the coast, but no definite locality was given. I have not seen any of the original material; but there are a number of specimens in the herbarium of the Arnold Arboretum that have been referred to it. It is often difficult to distinguish between this hybrid and × *Quercus atlantica*, although there is a greater tendency for the leaves to be lobed or toothed near the apex than in the latter.

VIRGINIA: Cape Henry, Princess Anne Co., *M. L. Fernald & Bayard Long* 4863, Sept. 12, 1935. GEORGIA: Dorchester, *T. G. Harbison* 23, June 21, 1917; Folkston, *T. G. Harbison* 71, July 16, 90, July 17, 1918; Lumber City, *T. G. Harbison* 1, May 30, Nov. 14, Dec. 16, 1917. FLORIDA: Gainesville, *T. G. Harbison* 69, 75, July 25, 1918; Alachua County, *T. G. Harbison* 101, June 20, 1919; Sebring, *T. G. Harbison* 62, July 30, 1918. ALABAMA: Cottondale, *T. G. Harbison* 41, 44, May 19, 1917. MISSISSIPPI: Mississippi City, *T. G. Harbison* 8, Oct. 28, 1917. TEXAS: Milano, Milam Co., *E. J. Palmer* 11712, April 27, 1917; Jacksonville, Cherokee Co., *E. J. Palmer* 8597, Sept. 21, 1915; Bryan, Brazos Co., *E. J. Palmer* 10731, 10748, Sept. 17, 1916, 13474, 13476, April 27, 1918; Huntsville, Walker Co., *V. L. Cory* 19524, Sept. 11, 1936.

× *Quercus Capesii* W. Wolf (*Q. nigra* × *Phellos*), *Castanea* 10: 91, 120. 1945.

The description of this hybrid was based on variants that appeared in a planting of seedlings grown from acorns of a cultivated tree of *Quercus Phellos* growing in an assemblage of *Q. nigra* specimens at St. Bernard

College, Alabama. The two species grow together over most of their wide range in the southern states and what appear to be spontaneous hybrids between them have been found in several places. Hybridization seems also to have taken place among cultivated trees at other stations. The hybrid may be a relatively frequent one, but it is usually difficult to recognize it with certainty because of similarities of extreme forms of the parent species, especially in the leaves of shoots and juvenile specimens, which are often eccentrically lobed and quite similar in both, and they may sometimes be mistaken for hybrids.

NEW JERSEY: Cape May Co., Bayard Long 7943, Oct. 29, 1912. SOUTH CAROLINA: Calhoun Falls, T. G. Harbison 19, May 20, 1918. CULTIVATED: Hort. C. S. Mann, Hartsboro, Penn., C. S. Sargent, Sept. 13, 1914; Borde Hill, Sussex, England, Stephensen R. Clarke, May 18, 1933; La Maulevrie, Angers, France, Antoine de Cugnac, Sept., 1922.

(?) \times *Quercus Cocksii* Sargent (*Q. obtusa* \times *velutina*), Bot. Gaz. 65: 459. 1918; Man. Trees N. Amer. ed. 2, 262. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 14. 1924.

The only material that I have seen of this hybrid is the type collection of two sheets, R. S. Cocks 4702, Pineville, La., April 18, 1917.

The specimens have young but nearly fully grown leaves and pistillate flowers. The leaves are mostly 7 to 15 cm. long and 2 to 6 cm. broad, lanceolate or rhombic in outline, with nearly entire, undulate or eccentrically lobed margins. There is no doubt that the plant is a hybrid, and the shape of the leaves indicates *Quercus obtusa* as one of the parents; but the character of the pubescence on the under surface of the leaves rather suggests *Q. falcata* as the other parent, and if that is the case, it would be a synonym of \times *Q. beaumontiana*. But in the absence of fruit it is perhaps best to leave it among the doubtfully authenticated hybrids.

\times *Quercus Comptonae* Sargent (*Q. lyrata* \times *virginiana*), Bot. Gaz. 65: 456. 1918; Man. Trees N. Amer. ed 2, 293. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 14. 1924.

Quercus lyrata \times *virginiana* H. Ness, Jour. Heredity 9: 265, fig. 6-8. 1918.—Yarnell, Jour. Arnold Arb. 14: 68. 1933.

This is one of the most interesting of the hybrid oaks both on account of its striking characters derived from the very distinct parent species, and because of the fact that it has been found growing spontaneously at several stations and has also been produced artificially under conditions that have permitted careful study. It is a handsome and ornamental tree of rapid growth and should be valuable in cultivation. Although the live oak is not hardy in this latitude and the overcup oak though hardy is far north of its native range, several seedlings of the hybrid grown from acorns sent by Miss Compton from Mississippi grew for several years in the Arboretum until lost by fire injury.

VIRGINIA: Williamsburg (planted on Courthouse Green, but transplanted from Virginia Beach where it was found spontaneous), J. T. Baldwin, Jr. 5612, Jan. 20, 1947. ALABAMA: Selma, ("at old house on plantation"), T. G. Harbison 10, April 20 and Oct. 21, 1915. MISSISSIPPI: Natchez, Miss C. C. Compton, many collections under nos. 12, 16, 18, 19, 26, 27, 28, 29, 32, 33, 34, 35, 38, 39, 43, 44, 45, and 47, in

1915 and 1916, *C. S. Sargent*, April 17, 1915, April 16, 1916. LOUISIANA: New Orleans, *R. S. Cocks*, Oct., 1911, *C. S. Sargent*, Audubon Park, March 31, 1917. TEXAS: along Payson's Creek, Matagorda Co., *C. H. Mohr* 96, Dec. 18, 1880.

A number of specimens from cultivated plants are also in the herbarium of the Arnold Arboretum, including several of the Ness hybrids grown at College Station, Texas, others grown here from acorns sent by Professor Ness and Miss Compton, and one from a small tree on the campus of the University of Kentucky, Lexington, Ky., that is said to have come originally from western Louisiana.

× *Quercus cravenensis* Little (*Q. incana* × *marilandica*), *Jour. Washington Acad. Sci.* 33: 9. 1943.

× *Quercus carolinensis* Trelease, *Proc. Amer. Phil. Soc.* 56: 48. 1917; *Mem. Nat. Acad. Sci.* 20: 14. 1924.—*Sargent, Man. Trees N. Amer.* ed. 2, 266. 1922. *Not. Q. carolinensis* Muench: 1770.

Quercus cinerea × *nigra* Ashe, *Jour. Elisha Mitchell Sci. Soc.* 11: 91. 1894.

Trelease gave no description and did not cite a type specimen when the name × *Quercus carolinensis* was published. But Ashe's notes on the plants and collections on which it was evidently based give a good idea of the hybrid. He stated that perhaps ten trees were seen, all in the neighborhood of the coast. I have not seen the original material, but several specimens in the herbarium of the Arnold Arboretum seem clearly to represent it. In typical specimens the pubescence and veining of the leaves show the relationship to *Quercus marilandica* and some of them have the subcordate base and short petioles characteristic of that species. The branchlets are generally stout and stiff, which is also a character of the black jack oak; but in other specimens the branchlets are more slender and the general shape of the leaves with long petioles and cuneate bases more nearly resembles the other parent.

VIRGINIA: south of Franklin, Southampton Co., *M. L. Fernald & Bayard Long* 8242, June 19, 1938 (G). NORTH CAROLINA: Carolina Beach, New Hanover Co., *R. H. Gorfry* 6241, Aug. 28, 1938 (G); New Berne, *T. G. Harbison* 27, 48, Oct. 9, 1917. SOUTH CAROLINA: Seneca, *T. G. Harbison* 6083, April 29, 1922; Myrtle Beach, *Ludlow Griscom* 16513, April 24, 1932. GEORGIA: Lumber City, *T. G. Harbison* 3, May 29, 4, May 8, and 1, Nov. 15, 1917; Climax, *T. G. Harbison* 3, May 29, 8, 10, Nov. 6, 1917. ALABAMA: Spring Hill, *T. G. Harbison* 5861, March 27, 1920; TEXAS: Fletcher, Hardin Co., *E. J. Palmer* 12741, Sept. 12, 1917.

(?) × *Quercus Deami* Trelease (*Q. alba* × *Muhlenbergii*), *Proc. Amer. Phil. Soc.* 56: 49. 1917; *Mem. Nat. Acad. Sci.* 20: 14. 1924.—*Sargent, Man. Trees N. Amer.* ed. 2, 302. 1922.—*Deam, Fl. Indiana* 384. 1940.

Quercus alba × *Muhlenbergii* Deam, *Rept. Ind. Bd. Forestry, Bull.* 2: 127. 1912.

In proposing the name × *Quercus Deami* for this hybrid Trelease referred to Deam's description and plate (22). The fine original tree on which it was based is now preserved as a state monument near Bluffton, Ind. It was believed to be a hybrid between *Quercus alba* and *Q. Muhlenbergii*, and was so determined by G. B. Sudworth. The leaves have more resemblance to those of *Quercus alba* in outline than to those of the other supposed parent, and they are pale and finely pubescent on the under surface. Some doubt has been thrown on the parentage by the fact that

seedlings raised at the Arnold Arboretum from acorns supposed to have come from the type tree have leaves similar to those of *Quercus bicolor*. Should it be found that the tree is really a cross between *Quercus alba* and *Q. bicolor*, the name would have to be regarded as a synonym of \times *Quercus Jackiana*. But since there may be a possibility of error in the record, it seems best to suspend judgment until there is more evidence. Irrespective of the parentage of the original plant, some of the collections enumerated below are probably crosses between *Quercus alba* and *Q. Muhlenbergii*.

PENNSYLVANIA: Waterside, Bedford Co., *David Berkheimer* 5486, Aug. 21, 1944. INDIANA: 3 miles northwest of Bluffton, Wells Co., *C. C. Deam* 14117, Sept. 28, No. 14131, Oct. 5, 1913, No. 22100, Sept. 24, 1916, No. 49948, Sept. 22, 1930 (all from the type tree). ILLINOIS: New Haven, White Co., *E. J. Palmer* 15298, May 28, 1919. KENTUCKY: Litchfield, Grayson Co., *W. W. Eggleston* 5444, Oct. 11, 1909 (G).

\times *Quercus Demarei* Ashe (*Q. nigra* \times *velutina*), *Jour. Elisha Mitchell Sci. Soc.* 41: 268. 1926.

Quercus nigra \times *velutina*? Palmer, *Jour. Arnold Arb.* 7: 119. 1926.

I have not seen the type specimen, but several collections in the herbarium of the Arnold Arboretum seem to be hybrids between the water-oak and the black oak.

ARKANSAS: Boto, Pike Co., *D. Demaree* 9395, Sept. 29, 1932; Craighead Co., *D. Demaree* 7180, Sept. 18, 1929; Hot Springs, Garland Co., *E. J. Palmer* 26858, April 22, 27117, May 19, 1925. LOUISIANA: Natchitoches, *E. J. Palmer* 7473, May 3, 1915.

\times *Quercus Egglestoni* Trelease (*Q. imbricaria* \times *Shumardii*), *Mem. Nat. Acad. Sci.* 20: 14. 1924.

\times *Quercus Shirlingii* Bush ex Palmer & Steyermark. (*Q. imbricaria* \times *Shumardii* var. *Schneckii*), *Ann. Missouri Bot. Gard.* 22: 521. 1935.

Trelease's brief description of \times *Quercus Egglestoni* says: "Very like \times *Q. runcinata* but with thicker leaves, the clay-colored or reddish buds intermediate between those of *maxima* and *Shumardii*." In giving the parentage he placed a question mark after *Q. imbricaria*. In the type specimen the leaves are deeply divided with sharp nearly simple symmetrical lobes, much more like those of *Q. Shumardii* than of the other suggested parent. The acorns are short-ovate to subglobose, 1.5–1.7 cm. long, with shallow cups enclosing about $\frac{1}{4}$ of the nut, and small closely imbricated glabrous scales, and they are somewhat intermediate between those of the suggested parents. If the name is accepted, it would have priority over \times *Q. Shirlingii*, as I do not think it possible to determine which variety of *Q. Shumardii* is involved in such a hybrid.

KENTUCKY: Litchfield, Grayson Co., *W. W. Eggleston* 5444, Oct. 11, 1909 (G). MISSOURI: Oak Grove, *B. F. Bush* 11637, Oct. 22, 1927.

\times *Quercus Eplingi* C. H. Muller (*Q. Douglasii* \times *Garryana*), *Amer. Midl. Naturalist* 19: 585. 1938.

The type specimen was collected by Epling and Robinson, Lake Co., California, July 27, 1935, and is deposited in the herbarium of the University of California, Los Angeles, Calif. I have not seen any material referable to it.

× *Quercus exacta* Trelease (*Q. imbricaria* × *palustris*), Proc. Amer. Phil. Soc. 56: 49. 1917; Mem. Nat. Acad. Sci. 20: 14. 1924.—Sargent, Man. Trees N. Amer. ed. 2, 268. 1922.

Quercus imbricaria × *palustris* Engelmann ex A. Braun, Sitzungsber. Gesellsch. naturf. freunde Dec. 20, 1870: 82. 1871; Bot. Zeit. 29: 202. 1871.—Engelmann, Trans. Acad. Sci. St. Louis 3: 400. 1877.

It is sometimes difficult to distinguish sterile specimens of this hybrid from × *Q. runcinata*. As compared with the latter, the leaves are inclined to be somewhat smaller and thinner in texture and to have fewer primary veins and more persistent tomentum in the axils of the veins and along the midrib. But all of these characters are variable and some specimens may be doubtful.

PENNSYLVANIA: Finland, Bucks Co., Bayard Long 18719, May 23, 1918 (G).

INDIANA: near Half Moon Pond, Posey Co., C. C. Deam 29116, Aug. 16, 1919.

ILLINOIS: near Olney, Richland Co., Robt. Ridgway 33, 34, Aug. 18, 1914, 1488, Sept. 29, 1921, C. S. Sargent, Oct. 5, 1913, E. J. Palmer 22625, May 15, 1923; Gentry Creek, Richland Co., Robt. Ridgway 27, Sept. 9, 1918; (East St. Louis?), George Engelmann, 1870 (G).

× *Quercus fallax* nom. nov.

Quercus macrocarpa × *Muhlenbergii* Hitchcock, Bot. Gaz. 18: 110–111, pl. 8. 1893.

— Bush, Garden and Forest 8: 32. 1895.—Sargent, Silva 8: 56. 1895.

Arbor foliis obovatis vel lanceolato-obovatis 8–24 cm. longis 4–12 cm. latis dentato-lobatis subtus pallidis plene minute pubescentibus. Fructus oblongo-obovatus 2–3 cm. longus et latus; glande in cupulo rotundo circiter $\frac{1}{2}$ inclusa, squamis cupulae acuminatis crassis pubescentibus.

Trelease proposed the name × *Quercus Hillii* for a hybrid that was supposed to have arisen between the two species mentioned above. Although no description was given and no type specimen cited, it is evident from the name and from a reference to a note in Sargent's Silva that it was based on a collection of E. J. Hill, near Roby, Indiana. But an examination of a sheet of Hill's collection in the herbarium of the Arnold Arboretum convinces me that it is really a hybrid between *Quercus bicolor* and *Q. macrocarpa*, a combination that was described later in the same paper by Trelease as × *Quercus Schuettei*. If that is the case, × *Quercus Schuettei* must be regarded as a synonym of the earlier name, and it is necessary to adopt a new name for the real hybrid between *Quercus macrocarpa* and *Q. Muhlenbergii*.

Professor A. S. Hitchcock (28) reported finding this hybrid near Manhattan, Kans., in 1893, and Mr. B. F. Bush (13) gave an account of two trees found near Independence, Mo., in 1895. I have not seen Hitchcock's collection, but the description and the figure that accompanied it show a plant very similar in foliage to *Quercus macrocarpa*. The fruit was described as intermediate between that of the parent species. In the specimen that is taken here as the type of × *Quercus fallax* and in other collections by Bush the leaves are clearly intermediate between those of the bur-oak and the chinquapin-oak. The fruit is nearly as large as the average in the bur-oak.

MISSOURI: Independence, Jackson Co., *B. F. Bush* 621, Sept. 11, 625, Sept. 16, 1894, 626, Oct. 14, and 629 (TYPE), Oct. 7, 1895; Swope Park (Kansas City), *B. F. Bush* 10326, Oct. 6, 1923.

× *Quercus Faxonii* Trelease (*Q. alba* × *prinoides*), Proc. Amer. Phil. Soc. 56: 49. 1917; Mem. Nat. Acad. Sci. 20: 14. 1924.—Sargent, Man. Trees N. Amer. ed. 2, 302. 1922.

There seems to be no reason to question the parentage of this hybrid although it may be difficult in some cases to distinguish sterile specimens from forms of × *Quercus Saulei*.

MASSACHUSETTS: East Walpole, *J. G. Jack* 1, Sept. 17, 1914, May 28, 1915, June 1, 1916, May 31, 1926, No. 2952, May 25, 1931. NEW YORK: Albany, *H. D. House* 20137, Sept. 2, 1932 (G).

× *Quercus Fernaldi* Trelease (*Q. borealis* × *ilicifolia*), Mem. Nat. Acad. Sci. 20: 15. 1924.

The parentage of this hybrid was given by Trelease as *Q. ilicifolia* × *maxima*, but in this writer's opinion, *Q. borealis* and *Q. maxima*, so-called, are only forms of varieties of one species, and it is generally impossible to tell which of them is involved in a hybrid. Sargent proposed the name × *Quercus Lowellii* (53) for a supposed hybrid between *Quercus borealis* and *Q. ilicifolia*. But an examination of the type, which was a sterile shoot, led Trelease to suggest that perhaps it was only an aberrant form of *maxima* or *borealis*; and I believe that he was correct in his opinion and that × *Quercus Lowellii* must therefore be considered a synonym of *Q. borealis*.

MASSACHUSETTS: Sharon, summit of Moose Hill, *J. G. Jack* 3818, 3819, June 20, 1926; East Walpole, *J. G. Jack* 3954, Sept. 13, 3955, Sept. 20, 1931, 1, 2, 3, May 15, 1936. VIRGINIA: Little Stony Mountain, Madison Co., *H. A. Allard*, Sept. 23, 1933 (G).

× *Quercus Fernowi* Trelease (*Q. alba* × *stellata*), Proc. Amer. Phil. Soc. 56: 49. 1917; Mem. Nat. Acad. Sci. 20: 15. 1924.—Sargent, Man. Trees N. Amer. ed. 2, 302. 1922.

Quercus alba × *stellata* Engelmann, Trans. Acad. Sci. St. Louis 3: 399. 1877.—Vasey, Bull. Torrey Bot. Club 10: 25, pl. 29–30. 1883.—Sargent (as *alba* × *minor*), Silva 8: 18, pl. 359. 1895.

NEW JERSEY: Browns Mills, Burlington Co., *J. C. Swartley* 429, Aug. 24, 1935.

VIRGINIA: Red Clay Creek, *C. S. Sargent*, Oct. 6, 1891; northwest of Suffolk, Nansemond Co., *M. L. Fernald* & *Bayard Long* 13321, July 23, 1941 (G); Beverley Hill to High Point, Fauquier Co., *H. A. Allard* 9794, Oct. 26, 1941 (G); Bull Run Mountains, Fauquier Co., *H. A. Allard* 9944, May 17, 1942 (G). DELAWARE: Marshallton, *J. P. Otis*, Oct. 1923. MARYLAND: near Beltsville, *L. P. McCollough*, Oct., 1943.

INDIANA: southeast of Nashville, Brown Co., *C. C. Deam* 56933, Oct. 10, 1935.

MISSOURI: Allenton, *G. W. Letterman*, May 10, 1882, Oct., 1883, April 30, July 10, 1884, Oct., 1890, *C. S. Sargent*, Aug. 26, 1894, *J. H. Kellogg*, Oct. 12, 1907, Oct. 5, 1910, 25978, June 14, 1932. TEXAS: Milano, Milam Co., *E. J. Palmer* 11658, April 24, 1917.

× *Quercus filialis* Little (*Q. Phellos* × *velutina*), Jour. Washington Acad. Sci. 33: 10. 1943.

× *Quercus inaequalis* Palmer & Steyermark, Ann. Missouri Bot. Gard. 22: 521. 1935. Not *Q. inaequalis* Watelet, 1866 (fossil).

× *Quercus dubia* Trelease, Proc. Amer. Phil. Soc. 56: 49. 1917; Mem. Nat. Acad. Sci. 20: 14. 1924. Not Ashe.

In his first paper on the hybrid oaks (64) Trelease gave the parentage of \times *Quercus dubia* Ashe as *Phellos* \times *?velutina*, and the same doubtful disposition of it was made in the Monograph of American Oaks, but in the latter work he suggested that *Q. laevis* might be one of the parents, and he also remarked that the type collection is very like the entire leaved form of \times *Q. Rudkini*, which it may represent. Sargent considered \times *Q. dubia* a hybrid between *Q. laevis* (*cinerea*) and *Q. laurifolia* — a wide divergence of opinion —, and it would seem that the name was well chosen. There is a large series of specimens under the name \times *Quercus dubia* in the herbarium of the Arnold Arboretum, including several sheets collected and named by Ashe, as well as others that he called \times *Q. atlantica* and one that was given the manuscript name of \times *Q. bladenensis*. A careful examination of this material leads me to believe that more than one and perhaps three or four hybrids are represented. But none of them suggest a cross between the willow-oak and the black oak. Certainly *Quercus laurifolia* is one of the parents in most cases, and there can be little doubt that *Q. laevis* is involved in many of them. And a few sheets can probably be referred to \times *Q. Rudkini* as suggested by Trelease.

\times *Quercus filialis* has frequently been confused with \times *Q. heterophylla* which it resembles closely in the shape of the variable leaves. It can be distinguished from that hybrid by the more persistent tomentum on the under surface of the leaves, especially along the principal veins and in their axils, and by its generally larger winter-buds with pubescent scales. The acorns when present are distinguishable by the looser pubescent scales of the cups.

NEW JERSEY: Woodbury, Isaac C. Martindale, Sept., 1876; Belleplain State Forest, Cape May Co., H. A. Scribner, Aug. 2, 1939; Mt. Holly, S. P. Sharples, Sept. 6, 1881. DELAWARE: Wilmington, A. Commons, Sept. 29, 1876, Sept. 16, 1877 (G). MISSOURI: Poplar Bluff, E. J. Palmer 16342 (type of *Q. inaequalis*), Sept. 11, 1919, 20676, Oct. 5, 1921. ARKANSAS: Hardinville, Faulkner Co., E. J. Palmer 26505; Conway, Faulkner Co., D. Demaree 13812, Oct. 2, 1936; Hot Springs, E. J. Palmer 29098, Oct. 10, 1925, 29577, Nov. 5, 1925. LOUISIANA: Plains, East Baton Rouge Parish, Clair A. Brown 9904, Oct. 13, 1943. Cultivated in the Arnold Arboretum.

\times *Quercus Ganderi* C. B. Wolf (*Q. agrifolia* \times *Kelloggii*), Proc. Calif. Acad. Sci. ser. 4, 25: 178, pl. 18-19. 1944.

A full description with numerous figures of the leaves and fruit accompanied the publication of this name. There were also notes on a number of trees discovered in San Diego Co., Calif., and on results obtained with seedlings grown from acorns of the type tree. Another collection was mentioned from Monterey County that may be of similar hybrid origin. The formula of parentage given by the author was, *Quercus Kelloggii* Newb. \times *Quercus agrifolia* var. *oxyadenia* (Torr.) J. T. Howell.

CALIFORNIA: between Santa Ysabel and Lake Henshaw, San Diego Co., C. B. Wolf 9487, Jan. 24, 1939, C. B. Wolf & P. C. Everett 9483, Jan. 10, 1939, 9543 (ISOTYPE), Oct. 20, 1939; from Mesa Grande on road to Lake Henshaw, San Diego Co., C. B. Wolf 9488, 9489, Jan. 24, 1939; south of Maretts on road to Santa Ysabel, San Diego Co., C. H. Muller 4034, Aug. 9, 1941.

× *Quercus garlandensis* Palmer (*Q. falcata* × *nigra*), Jour. Arnold Arb. 7: 119. 1926
(as *nigra* × *rubra*).

The description of this hybrid was based on material from two trees found near Hot Springs, Ark. Both supposed parents were growing in the immediate vicinity; and the intermediate characters of the foliage, fruit, bark, and winter-buds indicate the relationship. The leaves are extremely variable in shape and size, many of them being asymmetric; and the loose pale or tawny pubescence of the young leaves is significant. A few additional trees have been found in other localities.

ARKANSAS: Hot Springs, *E. J. Palmer* 23139, July 7, 24237, 24328, Oct. 20, 1923, 24455, 24456, April 22, 1924, 26856, 26857, April 22, 29223, Oct. 14, 29573, 29574, Nov. 5, 1925; Langley, Pike Co., *D. Demaree* 9515, Oct. 5, 1932. ALABAMA: Sardis, *R. S. Cocks* 4704, Sept. 25, 1917; Berlin, *R. S. Cocks*, Aug., 1917; Mt. Vernon, *T. G. Harbison* 8, May 19, 1917. LOUISIANA: Pineville, *R. S. Cocks* 4702, Oct. 3, 1917.

× *Quercus Giffordi* Trelease (*Q. ilicifolia* × *Phellos*), Proc. Amer. Phil. Soc. 56: 49. 1917; Mem. Nat. Acad. Sci. 20: 15. 1924.—Sargent, Man. Trees. N. Amer. ed. 255. 1922.

An isotype in the herbarium of the Arnold Arboretum consists only of a sterile shoot and several detached leaves. The outlines of the undulate or irregularly lobed leaves and the fine cinereous pubescence on their under surface seem to confirm the suggested parentage. The specimens from Delaware are much better, and some of them have mature fruit.

NEW JERSEY: May's Landing, *J. C. Gifford & J. E. Peters*, July 11, 1890 (ISOTYPE). DELAWARE: near Dover, *C. S. Sargent*, Oct. 10, 1922; Wilson Station, *J. T. Otis*, 1922; near Marshallton, *J. T. Otis*, Sept. 18, 1923.

× *Quercus guadalupensis* Sargent (*Q. macrocarpa* × *stellata*), Bot. Gaz. 65: 454. 1918; Man. Trees N. Amer. ed. 2, 291. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 15. 1924.

Although only material from the type tree is known, it is so complete and the leaves and fruit are so clearly intermediate between those of the parent species that there can be no doubt as to its origin. Both the bur-oak and the post-oak were found growing near the type tree.

TEXAS: Fredericksburg Junction, Kendall Co., *E. J. Palmer* 10878 (TYPE), Oct. 1, 1916.

× *Quercus Harbisonii* Sargent (*Q. stellata* × *virginiana*), Bot. Gaz. 65: 458. 1918
(as *stellata* var. *Margareta* × *virginiana* var. *geminata*); Man. Trees N. Amer. ed. 2, 295. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 15. 1924 (as *geminata* × *Margareta*).

× *Quercus neo-tharpii* A. Camus (as *Durandii* × *virginiana*), Les Chênes 2: 754. Atlas 2: pl. 226, fig. 9–19. 1939.

Although Sargent described × *Quercus Harbisonii* as a hybrid between botanical varieties of the post-oak and live oak, other specimens have been found that show evidences of being crosses between the typical forms of these species, and I can see no way of distinguishing them. If *Quercus geminata* and *Q. Margareta* were regarded as distinct species, as was held by Trelease and others, the name × *Quercus Harbisonii* would technically have to be restricted to a cross between them and it would be necessary to adopt another name for the *Q. stellata* × *virginiana* hybrid. Besides

several spontaneous specimens of apparent crosses between typical forms of the post-oak and live oak, it has been produced by artificial cross-pollination, as mentioned in the introduction.

Specimens of Tharp's collections from the coast of Texas that were cited and illustrated by Camus as believed to be a hybrid between *Quercus Durandii* and *Q. virginiana* are in the herbarium of the Arnold Arboretum. Except for a superficial resemblance in the shape of some of the leaves, I can see no suggestion of *Quercus Durandii* parentage in them. The fruit closely resembles that of *Q. virginiana*, but it is large and with deep cups even for that species. The scurfy stellate pubescence on the under surface of the mature leaves and on the branchlets suggests *Q. stellata* as the other parent.

FLORIDA: Jacksonville, *T. G. Harbison* 16, Dec. 3, 1917 (TYPE). TEXAS: Ft. Chadburn, Coke Co., *E. J. Palmer* 12463, July 9, 1917; Roby (Fisher Co.), *B. C. Tharp* 4238, Aug. 16, 1926; between Seadrift and Port O'Connor, *B. C. Tharp* 8768-a, Dec. 1, 1928, 8768-b, March 20, 1930; College Station (artificial hybrids, cultivated), *H. Ness*, 1922, and *W. S. Flory Jr.*, 1943.

(?) \times *Quercus Hastingsii* Sargent (*Q. marilandica* \times *Shumardii*). Bot. Gaz. 65: 450. 1918; Man. Trees N. Amer. ed. 2, 259. 1922 (as *Q. marilandica texana*).

The leaves of the type, except in their fewer shallow and blunt lobes, are much nearer in appearance to those of *Quercus Shumardii* var. *texana* than to those of the other supposed parent, and Trelease held that it was apparently scarcely more than a form of *Q. texana*. But there are indications of hybrid origin and of the influence of *Q. marilandica* in the stiff branchlets, pubescent through the first year, and in traces of pubescence on the petioles, the under surface of the leaves, cup scales, and scales of the winter-buds. Specimens found at Brownwood, Texas, more nearly resemble *Q. marilandica* var. *Ashei* Sudw. in the shape of the leaves and in the stiff habit and dark rough bark. The supposed hybrids have all been found in the vicinity of *Q. Shumardii* var. *texana* and *Q. marilandica* or the variety *Ashei*, growing under xerophytic conditions. Should hybrids be found between the typical varieties of the two species, they might differ rather widely from \times *Quercus Hastingsii* as found in Texas.

TEXAS: near Bourne, *S. H. Hastings* 145 (TYPE), Oct., 1910; Brownwood, *E. J. Palmer* 10364, July 5, 1916, 13056, Oct. 18, 1917, 26818, Nov. 1, 1924, 29547, 29548, Nov. 2, 1925.

\times *Quercus Hawkinsii* Sudworth (*Q. borealis* \times *velutina*), Amer. Forestry 23: 685, fig. 1, 2, 5. 1917.

Quercus Porteri Trelease, Proc. Amer. Phil. Soc. 56: 51. 1917 (nomen nudum); Mem. Nat. Acad. Sci. 20: 16. 1924.

In publishing the description of \times *Quercus Hawkinsii* with full notes and figures, Sudworth gave his reasons for believing that it was a hybrid between *Quercus borealis* and *Q. velutina*. But he also suggested the possibility that *Quercus palustris* might be one of the parents. The acorns figured certainly resemble those of the pin-oak, but the leaves and bark are more like those of the black oak. If, as seems probable, the parentage was correctly determined, the name has priority over \times *Quercus Porteri*.

For although Trelease's first publication of the name \times *Quercus Porteri* was a few months earlier, the description of \times *Q. Hawkinsii* appeared first.

Trelease in his Monograph of American Oaks accepted *Quercus borealis* and *Q. maxima* as distinct species, and he gave the parentage of \times *Q. Porteri* as *Q. maxima*? \times *velutina*. He also inserted the name \times *Quercus Hawkinsii* with the parentage, *Q. borealis* (*maxima*) \times *velutina*, but with the note: "Scarcely differs from *maxima* except in its yellow cotyledons."

The leaves of the northern red oak and the black oak are generally quite similar in shape, and a hybrid between them is not outstanding or easily distinguished in foliage specimens. The only notable distinction between the typical form of *Quercus borealis* and the variety *maxima* is in the shape of the acorn cups, and, in my opinion, it would generally be impossible to determine which variety is involved in a hybrid. The best characters for distinguishing \times *Quercus Hawkinsii* from *Q. borealis* are found in the somewhat pubescent scales of the winter-buds and in the more persistent tomentum on the under surface of the leaves. If acorns are available, they are likely to show characters of the black oak in the shape of the cup or in the pubescence of its inner surface and scales.

MAINE: Lyman, York Co., *F. Hyland* 162, July 24, 1934. MASSACHUSETTS: Jamaica Plain, *J. G. Jack* 3803, Nov. 2, 1925; Dedham, *J. G. Jack* 3839, Oct. 15, 1926. NEW YORK: Durand-Eastman Park, Rochester, *B. H. Slavin* 6, Oct. 12, 1918. PENNSYLVANIA: Easton, *Thos. C. Porter*, Sept. 30, 1893, May 12, 1894. OHIO: Lakeside, Ottawa Co., *W. A. Kellerman* 63, May 17 and Sept. 16, 1900. MISSOURI: Swope Park (Kansas City), *Kendall Laughlin*, 1938; Holmes Park (Kansas City), *B. F. Bush* 9944, Oct. 9, 1922, *E. J. Palmer* 22327, Oct. 21, 1922; Dumas, Clark Co., *E. J. Palmer* 21904, Sept. 8, 1922, *B. F. Bush* 9528, Aug. 29, 1921; Crowley's Ridge, Dunklin Co., *J. H. Kellogg* 26043, Aug. 7, 1932. This hybrid is also in cultivation in the Arnold Arboretum, and specimens grown from seeds have retained the intermediate characters.

\times *Quercus heterophylla* Michx. f. (*Q. borealis* \times *Phellos*), *Hist. Arb. Amer.* Sept. 2: 87, pl. 16. 1812; *N. Amer. Silva* (English ed.) 1: 75, pl. 18. 1819.—Gale, *Proc. Nat. Inst.* 1875: 70, fig. 1. 1875.—Sargent, *Silva* 8: 456, pl. 436. 1895; *Man. Trees N. Amer.* ed. 2, 263, fig. 241. 1922.—Trelease, *Proc. Amer. Phil. Soc.* 56: 49. 1917; *Mem. Nat. Acad. Sci.* 20: 15. 1924.

This classic example of a spontaneous hybrid oak has been figured and described many times. A discussion will be found in the introduction to this paper.

NEW YORK: Tottenville, Staten Island, *Arthur Hollick*, Sept. 2, 1888, *J. K. Small*, Aug. 2, 1890, *C. S. Sargent*, Aug. 6, 1894. PENNSYLVANIA: Hatboro, *C. S. Mann*, Oct., 1918; Upper Darby, *Joseph Crawford*, Aug. 30, 1909; Finland, *W. A. Kline*, July and Nov. 3, 1917. NEW JERSEY: Mickleton, Gloucester Co., *B. Heritage*, Oct. 22, 1895; Gloucester Co., *C. A. Gaskell*, Aug. 1914; State Game Farm, Ocean Co., *Hollis Koster*, June 30, 1937; Buss River State Forest, Burlington Co., *Hollis Koster*, May 13 and Oct. 3, 1934; Westville, *J. W. Adams* 4186, Nov. 2, 1937; South Westville, *J. W. Adams* 4562, Oct. 21, 1938; Mullica Hill, Gloucester Co., *J. W. Adams* 4853, Oct. 10, 1939. DELAWARE: Hazletville, *J. P. Otis*, 1922; Marshallton, *J. P. Otis*, Sept. 18, 1923. MISSOURI: northwest of Wappapello, Wayne Co., *Julian A. Steyermark* 6428, Sept. 2, 1938; Crowley's Ridge, Dunklin Co., *J. H. Kellogg* 26039, Aug. 7, 1932. ARKANSAS: Corning, *G. W. Letterman* 4, Oct. 1882. OKLAHOMA: Page, Le

Flore Co., *E. J. Palmer* 20901, April 22, 21597, May 30, 22232, Oct. 7, 1922. Specimens have also been examined from trees cultivated in the Arnold Arboretum and in a number of other botanic gardens and parks, including seedling plants grown from cuttings from the original tree.

× *Quercus Hillii* Trelease (*Q. bicolor* × *macrocarpa*), Proc. Amer. Phil. Soc. 56: 49. 1917 (as *macrocarpa* × *Muhlenbergii*); Mem. Nat. Acad. Sci. 20: 15. 1924.—Sargent, Silva 8: 56. 1895; Man. Trees N. Amer. ed. 2, 292. 1922.—Deam, Fl. Indiana, 384. 1940.

× *Quercus Schuettei* Trelease, Proc. Amer. Phil. Soc. 56: 51, pl. 2-3. 1917.

The synonymy was discussed under description of × *Quercus fallax*. × *Quercus Hillii*, as here understood, seems to be a relatively abundant and widely distributed hybrid, since the parent species are rather closely related and grow together in similar habitats over a large area. The leaves of both species are quite variable in shape, but those of the bur-oak (*Q. macrocarpa*) are usually larger, more deeply lobed and with a looser less persistent pubescence than in *Q. bicolor*. Leaves of the hybrid show intermediate characters, but fruit may be necessary to make determination certain in some cases.

CANADA: Montreal, near Rockfield, *J. G. Jack*, Aug. 17, 1894; Chateaugay, *J. G. Jack*, Sept. 16, 1911, Aug. 15, 1895, Sept. 7, 1896; Longueuil, *M. Victorin* 16477, Sept., 1922. NEW YORK: Golah (Monroe Co.), *J. Dunbar*, Sept. 28, 1915, Sept. 23, 1922; Mumford, Monroe Co., *B. H. Slavin* 47, Sept. 27, 1922. INDIANA: Roby, (Lake Co.), *E. J. Hill*, May 12 and 27, June 27, 1892 (TYPE). Cultivated, Arnold Arboretum, Municipal Parks, Rochester, N. Y., and elsewhere in America and Europe.

× *Quercus humidicola* Palmer (*Q. bicolor* × *lyrata*), Jour. Arnold Arb. 18: 140. 1937.

The swamp white oak and the overcup oak, both trees of low wet woods, are often found growing together in regions where their ranges overlap. The leaves and fruit of the two species are quite different, and hybrids are rather easily recognizable by their intermediate characters.

ILLINOIS: Mounds, Pulaski Co., *E. J. Palmer* 16634, Oct. 1, 1919, 19546, Oct. 16, 1920; Mound City, Pulaski Co., *E. J. Palmer* 16642, Oct. 1, 1919, 19549, 19550, Oct. 16, 1920; northwest of Wynoosie, Richland Co., *Robt. Ridgway* 777, Aug. 27 and Sept. 7, 1919; Little Wabash River, s. e. corner Clay Co., *Robt. Ridgway* 1557, Oct. 12, 1921. MISSOURI: Campbell, (Dunklin Co.), *B. F. Bush* 6365 (TYPE), Oct. 6, 1910.

× *Quercus inconstans* Palmer (*Q. Emoryi* × *hypoleucoides*), Jour. Arnold Arb. 10: 34. 1929.

× *Quercus livermorensis* Muller, Amer. Midl. Naturalist 19: 585. 1938.

Two shrubby plants believed to be this hybrid were found near the head of a rocky ravine east of Livermore peak, in the Davis Mountains, at an altitude of about 2000 meters. Both supposed parent species were growing near by. The intermediate characters of the leaves indicate the hybrid origin of the plant, as well as the association and its rarity. The leaves are oblong-elliptic to oblanceolate in outline, mostly 4-8 cm. long and 2-4 cm. wide, with 2-3 or rarely 4 pairs of pungent, bristle-tipped teeth, coriaceous or subcoriaceous, with slightly revolute margins, green and thinly stellate-pubescent above, coated beneath with thick, pale, rather easily detached tomentum; veins slightly impressed above, prominent

beneath; petioles 6–10 mm. long. The pistillate flowers are borne on short hairy peduncles or are nearly sessile. No acorns were found. The leaves resemble those of *Quercus Emoryi* in the toothed margins, but they are mostly cuneate or narrowed and rounded at the base, as in *Q. hypoleucoides*. They also resemble the latter in the pale felty tomentose under surface. The fact that the tomentum is loosely attached and can be rubbed off with the finger is particularly significant, as this is often the case in hybrids between a glabrous and a strongly pubescent species.

TEXAS: Davis Mountains, Jeff Davis Co., *E. J. Palmer* 30934 and 30935 (TYPE), June 15, 1926; Davis Mountains, near Mt. Livermore, *L. C. Hinckley*, May 1, 1937 (G).

✗ *Quercus Jackiana* Schneider (*Q. alba* × *bicolor*), *Ill. Handb. Laubh.* 1: 202. 1904.
— Trelease, *Mem. Nat. Acad. Sci.* 20: 15. 1924.— Sargent, *Man. Trees N. Amer.* ed. 2, 302. 1922.

The type tree of this hybrid was discovered by Professor J. G. Jack in Franklin Park, Boston, Mass., growing in native woods. It has since been found at several other stations in this and other states. The leaves are more or less intermediate in outline between those of the parent species, but generally have more resemblance to those of the white oak, with deep nearly simple lobes or with the middle or upper pairs sometimes slightly broadened and indented at the apex, and with the under surface of the blades covered with a more or less dense tomentum, similar to that of *Quercus bicolor*. The fruit is sometimes nearly sessile, resembling large-fruited forms of the white oak except for the deeper cups, or it may be peduncled as in the swamp white oak.

MASSACHUSETTS: Franklin Park, Boston, *J. G. Jack*, Sept. 12, 1895, Sept. 14, 1902, Sept. 18, 1904, Sept. 20, 1916, Jan. 21, 1926, *C. E. Faxon*, Sept. 20, 1916; East Walpole, *J. G. Jack* 3924, Sept. 25, 1929; between Jamaica Plain and Dedham, *H. J. Koehler*, Aug. 18, 1925. RHODE ISLAND: near Diamond Hill, Providence Co., *E. J. Palmer* 46915, Sept. 11, 1943. NEW YORK: Black Rock Forest, Cornwall on Hudson, *H. H. Tryon* 1, 2, 1903. INDIANA: northeast of Onward, Cass Co., *C. C. Deam* 51066, Sept. 18, 1931. ILLINOIS: Coulterville, Randolph Co., *E. J. Palmer* 17090, Oct. 24, 1919. This hybrid is also in cultivation in the Arnold Arboretum.

✗ *Quercus jolonensis* Sargent (*Q. Douglasii* × *lobata*), *Bot. Gaz.* 65: 456. 1918; *Man. Trees N. Amer.* ed. 2, 248, 1922.— Trelease, *Mem. Nat. Acad. Sci.* 20: 15. 1924.

With leaves smaller and usually less deeply divided than in *Quercus lobata*.

CALIFORNIA: between King City and Jolon, *A. Eastwood* 44, Sept. 17, 155, 156, 163, Sept. 18, 1894, 164 TYPE, 165, Sept. 22, 1894.

✗ *Quercus Joorii* Trelease (*Q. falcata* × *Shumardii*), *Mem. Nat. Acad. Sci.* 20: 15. 1924.

I have not seen the type specimen nor any material that can be referred to this hybrid. *Quercus Shumardii* was questioned as one of the parents in the original publication, but the characters given in the brief description seem to indicate that it was correctly placed. The parent species grow together over a wide range, and it is to be expected that hybrids would appear. The type specimen was collected by Joor at Galveston, Texas, Sept. 25, 1884, according to Trelease.

✓ \times *Quercus Leana* Nuttall (*Q. imbricaria* \times *velutina*), *Sylva N. Amer.* 1: 13, pl. 5 bis. 1819.—Sargent, *Silva* 8: 176, pl. 434. 1895; *Man. Trees N. Amer.* ed. 2, 268. 1922.—Trelease, *Proc. Amer. Phil. Soc.* 56: 50. 1917; *Mem. Nat. Acad. Sci.* 20: 15. 1924.

The history and characters of this widely distributed hybrid were discussed in the introduction. In many cases it appears to come true to type in seedlings.

PENNSYLVANIA: Hyndman, Bedford Co., *J. K. Small*, Aug. 19-23, 1890. MARYLAND: Burnt Mills, *H. W. Henshaw*, Aug. 31, 1887 and May 6, 1888. DISTRICT OF COLUMBIA: Carroll Estate, *H. W. Henshaw*, June 21, 1886; Washington, *Lester F. Ward*, Sept., 1888, *George Vasey*, 1876. NORTH CAROLINA: near Biltmore, ex Herb. Biltmore, no. 821, April 25, Aug. 6 and Oct., 1896, no. 421-b, April 30, Sept. 11 and Oct. 11, 1897; Franklin, *C. S. Sargent*, Sept. 25, 1885, *F. E. Boynton*, 1893; Charlotte, Swaine Co., *C. S. Sargent*, 1885. MICHIGAN: northwest of Ann Arbor, *J. H. Eihlers* 3597, Oct. 16, 1927. OHIO: Cedar Point, Erie Co., *W. A. Kellerman*, July 19, 1899; Youngstown, Mahoning Co., *R. E. Horsey* 669, Sept. 28, 1917, Oct. 2, 1918. INDIANA: south of Bedford, Lawrence Co., *Ralph M. Kriebel* 1443, Oct. 18, 1933; near Bedford, *C. C. Deam* 10240, Oct. 14, 1911; Crown Point, Lake Co., *C. C. Deam* 18088, Aug. 23, 1911; southwest of Mt. Vernon, Posey Co., *C. C. Deam* 56919, Oct. 7, 1935; northwest of Mt. Summit, Henry Co., *J. L. Kirling* 4069, Sept. 18, 1936. ILLINOIS: Willow Springs, *E. J. Hill*, July 16, 1890, Oct. 16, 1891, May 23, 1892; near Olney, Richland Co., *Robt. Ridgway* 1321, Oct. 8, 1920; Marion Township, Richland Co., *Robt. Ridgway* 3068, July 22, 1928; Simpson, Johnson Co., *E. J. Palmer* 16670, Oct. 3, 1919, 19580, Oct. 23, 1920; Peters Creek, Hardin Co., *E. J. Palmer* 15467, June 10, 1919, 17035, Oct. 12, 1919, 19590, Oct. 27, 1920. KENTUCKY: Bowling Green, *S. F. Price*, 1902. MISSOURI: Independence, Jackson Co., *B. F. Bush* 94, Nov. 6, 1894; Swope Park (Kansas City), *B. F. Bush* 10243, Nov. 6, 1923, *E. J. Palmer* 24377, Nov. 5, 1923; Greenwood (Jackson Co.), *B. F. Bush* 10331, 10331-a, Sept. 5, 1924, *E. J. Palmer* 26033, Sept. 5, 1924; Washington Co., *G. W. Letterman*, Aug., 1877; Hog Hollow, Jefferson Co., *J. H. Kellogg* 25980, June 14, 1932; Hannibal, Marion Co., *E. J. Palmer* 20393, Sept. 7, 1921; Arcadia, Iron Co., *E. J. Palmer* 30232, May 21, 1926; Mine La Motte, Madison Co., *E. J. Palmer* 31574, Sept. 6, 1926; Greenfield, Dade Co., *E. J. Palmer* 10573, Aug. 5, 1916; between Fairport and Maysville, DeKalb Co., *Palmer & Steyermark* 41389. Cultivated in the Arnold Arboretum and in other botanical gardens and parks in America and Europe.

✓ *Quercus ludoviciana* Sargent (*Q. falcata* \times *Phellos*), *Trees and Shrubs* 2: 222. 1913; *Man. Trees N. Amer.* ed. 2, 264. 1922.—Trelease, *Mem. Nat. Acad. Sci.* 20: 16. 1924.

✓ *Quercus falcata* Ashe, *Jour. Elisha Mitchell Sci. Soc.* 11: 94. 1898. Not Michaux. 1801.

✓ *Quercus subfalcata* Trelease, *Proc. Amer. Phil. Soc.* 56: 52. 1917.

✓ *Quercus ludoviciana* var. *subfalcata* Rehder, *Jour. Arnold Arb.* 7: 240. 1926.

The parentage of this hybrid was given in the original description as *Quercus pagodaefolia* \times *Phellos*. But in later publications *Quercus pagodaefolia* was held by Sargent to be a variety of *Q. falcata*. If this disposition is correct, as in my opinion it is, only one inter-specific hybrid can be recognized. Rehder proposed, as cited above, to restrict the name to the cross between *Q. falcata* var. *pagodaefolia* and *Q. Phellos*. But an examination of a series of specimens does not show any satisfactory way of determining which variety of the southern red oak was involved in the type specimens or in other collections.

GEORGIA: Traders Hill, Charlton Co., *J. K. Small*, June 12-15, 1895. KENTUCKY: Wickliffe, Ballard Co., *E. J. Palmer* 16507, Sept. 20, 1919. MISSOURI: Campbell,

(Dunklin Co.), *B. F. Bush* 610-b, July 28, 1895. ARKANSAS: near Little Rock, *Geo. M. Merrill* 1413, Nov. 2, 1938; Piggott, Clay Co., *Delzie Demaree* 4154, April 11, 1927; Brinkley, Monroe Co., *Delzie Demaree* 10873, Aug. 30, 1934; banks of Little Missouri River, Pike Co., *Delzie Demaree* 9397, Sept. 29, 1932; near Conway, Faulkner Co., *Delzie Demaree* 10093, 10097, Nov. 4, 1932; McNab, Hempstead Co., *E. J. Palmer* 22466, April 25, 1923; 24013, Oct. 4, 1923, 29437, Oct. 28, 1925; Fulton, *B. F. Bush* 5693, March 23, 5833, June 11, 1909. MISSISSIPPI: Bay St. Louis, *R. S. Cocks*, Sept. 1923. LOUISIANA: Peterville, w. of Opeleusas, *C. S. Sargent*, April 4, Oct. 10, 1913 (TYPE); Lafayette, *Clair A. Brown* 9795, Aug. 30, 1943. ALABAMA: near Sardis, *R. S. Cocks* 814, July 30, 938, Sept. 17, 1915. TEXAS: Houston, *E. J. Palmer* 12754, Sept. 15, 12769, Sept. 16, 12774, Sept. 17, 1917. This hybrid has not proved hardy at the Arnold Arboretum.

(?) \times *Quercus ludoviciana* var. *microcarpa* (Dippel) Rehder, Jour. Arnold Arb. 7: 239. 1926.

Quercus Phellos microcarpa Dippel, Handb. Laubh. 108, fig. 49, 1892.

\times *Quercus subfalcata* var. *microcarpa* Sargent, Bot. Gaz. 65: 454. 1918.

Sargent's description of this ambiguous hybrid and the notes on it by Rehder under the name accepted here were based on trees cultivated in the Arnold Arboretum and obtained from the nurseries of Wezelburg and Sons, Hazerswaoude, Holland, in 1903, under the name of *Quercus chinensis microcarpa*. It appears to have been in cultivation in European gardens for many years under this name or as *Q. microcarpa*, *Q. robur microcarpa*, or *Q. Phellos microcarpa*. The origin of the plant is unknown and its relationship seems to be very doubtful. *Quercus Phellos* appears to be one of the parents, but there is little to suggest any known form of *Q. falcata*. The leaves are mostly linear-lanceolate or oblong-lanceolate in outline, of approximately the size and relative length and breadth of those of the willow-oak, but nearly all of them are toothed or lobed on the margins with sharp or obscure bristle-tipped projections. On some blades the lobes or teeth are symmetric and paired and on others they are very irregular. The young branchlets and the under surface of the young leaves are covered with a pale, easily detachable pubescence, but they become quite glabrous late in the season. The acorns are similar in shape to those of the willow-oak, but are smaller than the average for that tree. It is possible that the plant may have arisen as a cross between *Quercus incana* and *Q. Phellos*. But as the leaves in typical forms of both of these species are entire, it would not be expected that a hybrid between them would have toothed or lobed leaves. It may also be noted that *Quercus incana* has not been successfully grown at the Arnold Arboretum, but the hybrid appears to be perfectly hardy, as is also the willow-oak. While it seems to me to be quite unlikely that this supposed hybrid originated from a cross in which any form of *Quercus falcata* was involved, it is perhaps best in the absence of any positive evidence to leave it under its present name. The trees in the Arboretum often produce good crops of acorns, and it is possible that if a series of seedlings was grown from them, some significant results might be obtained.

\times *Quercus macnabiana* Sudworth (*Q. Durandii* \times *stellata*), Check List Forest Trees U. S. 103. 1927.

Quercus Durandii \times *stellata* Palmer, Jour. Arnold Arb. 4: 21. 1923.

Quercus Mahloni Palmer (as *Q. breviloba* \times *stellata*), Jour. Arnold Arb. 18: 139. (correction p. 361). 1937.

Two trees of \times *Q. macnabiana* were found growing with the supposed parent species; and a series of specimens with young and mature leaves, flowers, and fruit clearly indicates the parentage. The name \times *Quercus Mahloni* was proposed for a hybrid between the shrubby variety of *Q. Durandii* and *Q. stellata*, collected in the Arbuckle Mountains, Oklahoma, by George Mahlon Merrill. The typical variety of *Quercus Durandii* is not found in the region, and there can be no doubt that one of the parents was *Q. Durandii* var. *breviloba* (Sarg.) Palmer. But there are no clear characters except the shrubby habit and smaller size of the leaves to distinguish it from \times *Quercus macnabiana*, and it may consistently be placed under the earlier name.

ARKANSAS: McNab, Hempstead Co., *E. J. Palmer* 8965, Oct. 10, 1915, 12659, 12662, Sept. 6, 1917, 20645, Sept. 26, 1921, 20715, April 6, 1922, 29442, Oct. 28, 1925.

OKLAHOMA: Platt National Park, Murray Co., *G. M. Merrill* 1634, Oct. 28, 1935.

TEXAS: Strawn, Paolo Pinto Co., *E. J. Palmer* 14267, June 27, 1918; Brownwood, Brown Co., *E. J. Palmer* 29501, Nov. 1, 1925.

\times *Quercus Mellichampi* Trelease (*Q. laevis* \times *laurifolia*), Proc. Amer. Phil. Soc. 56: 50. 1917; Mem. Nat. Acad. Sci. 20: 16. 1924. — Sargent, Bot. Gaz. 65: 451. 1918; Man. Trees N. Amer. ed 2, 254. 1922.

Quercus Catesbeiae \times *laurifolia* Engelmann, Trans. Acad. Sci. St. Louis 3: 539. 1877.

The leaves in this hybrid are extremely variable and often eccentrically lobed.

SOUTH CAROLINA: Bluffton, *J. H. Mellichamp*, April 13 and Nov. 19, 1895, *C. S. Sargent*, Oct. 4, 1894; Port Royal, *T. G. Harbison* 15, Dec. 8, 1917. FLORIDA: Jacksonville, *T. G. Harbison* 28, Dec. 3, 1917, *A. D. Jackson*, Dec., 1923; Eustis, *T. G. Harbison* 12, June 22, 1919; San Mateo, *T. G. Harbison* 35, Dec. 6, 1917; near Gainesville, *W. A. Murrill*, Jan. 22, 1940; Orlando, *C. H. Baker* 2, April 5, 1915; Plymouth, *T. G. Harbison* 23, 24, Nov. 26, 1916; Zellwood, *T. G. Harbison* 25, 26, 27, 28, 29, Nov. 26, 1916; 2, Dec. 4, 1917.

\times *Quercus Morehus Kellogg* (*Q. Kelloggii* \times *Wisleszeni*), Proc. Calif. Acad. Sci. 2: 36. 1863. — Greene, W. Amer. Oaks 3, 47, 49, pl. 2. 1889. — Sargent, Silva 8: 120, pl. 407. 1895; Man. Trees. N. Amer. ed. 2, 271. 1922.

\times *Quercus moreha* Trelease, Proc. Amer. Phil. Soc. 56: 50. 1917.

CALIFORNIA: Newcastle (Placer Co.), *T. S. Brandegee*, Sept., 1886, July 5 and 21, 1889, *Alice Eastwood*, Sept. 9, 1894, 142, Sept. 12, 1894; Auburn, *Engelmann & Sargent*, Oct. 10, 1880, *Mary E. P. Ames*, Feb. 1894; San Bruno Hills, San Mateo Co., *G. Ward*, April 12, 1941; Mt. Tamalpais (Marin Co.) *A. Eastwood* 139, 140, Sept. 15, 1894, *Rimo Bacigalupi*, Nov. 12, 1922; Sausalito (Marin Co.), *A. Eastwood* 141, Sept. 15, 1894, 278, June 9, 1912, April, 1920, April 1, 1921, *Lewis S. Rose* 33072, April 12, 1933; Clinton, Amador Co., *Geo. Hansen* 916, April 29, 1892, Sept. 15, 1895; Middle Fork, Amador Co., *Geo. Hansen* 1197, April 27, 1892, 1231, Aug. 17, 1895; Pine Grove, Amador Co., *Geo. Hansen* 914, April 2, 1894, Irishtown, Amador Co., *Geo. Hansen* 915, Aug. 12, 1895; Hetch Hetchy Valley, Tuolumne Co., *C. M. Belshaw* 25, Aug. 2, 1935; between Auburn and Folsom, Sacramento Co., *C. B. Wolf* & *B. D. Stark* 5485, Sept. 24, 1933, *C. B. Wolf* 8341, March 30, 1937; west of Laytonville, Mendocino Co., *Joseph P. Tracy* 15198; Oct. 11, 1936; Ukiah, Mendocino Co., *Alice Eastwood* 3279, June 13, 1913; between Oathill and Mt. Sanhedrin, Lake Co., *Alice Eastwood* 12951, May 25, 1925; 12 miles north of Sacramento, *Wm. Vorriede*, Oct., 1927; Doane Valley, Palomar Mt., San Diego Co., *C. H. Muller* 4026, Aug. 9, 1941; summit of Palomar Mt., *C. H. Muller* 4031, Aug. 9, 1941.

× *Quercus moultonensis* Ashe (*Q. Phellos* × *Shumardii*), *Rhodora* 24: 78. 1922.

The two species given as parents of this hybrid are often found growing together throughout their common range in the coastal plain and the lower Mississippi Valley. Ashe's description was based upon specimens from the Moulton Valley, of the Tennessee River in Lawrence Co., Tennessee. I have not seen the type material, but several specimens in the herbarium of the Arnold Arboretum appear to belong here.

VIRGINIA: Suffolk, *Alfred Rehder*, Aug. 21, 1908. ARKANSAS: Bayou Bartholomew, Jefferson Co., *Delzie Demaree* 13939, Oct. 11, 1936; Newport, Jackson Co., *Delzie Demaree* 20385, Aug. 26, 1939; Rowland, Pulaski Co., *Delzie Demaree* 8833, Oct. 30, 1931; Conway, Faulkner Co., *Delzie Demaree* 10086, Nov. 4, 1932.

× *Quercus mutabilis* Palmer & Steyermark (*Q. palustris* × *Shumardii*), *Ann. Mo. Bot. Gard.* 22: 521. 1935.

The description was based upon specimens from a single tree found growing with *Quercus palustris* and *Q. Shumardii* var. *Schneckii* in western Missouri, and the latter was given as one of the parents. However, as in other cases, it does not seem practicable to distinguish which particular variety of a species is involved in a hybrid. So the name should be considered applicable to hybrids between any varieties of the parent species. The leaves and the fruit resemble more closely those of *Quercus Shumardii* than of the other parent, but the bark and habit of the tree and the thin shallow cups of the acorns indicate hybridization with *Q. palustris*. The leaves of some of the other specimens cited below have more resemblance to those of *Quercus palustris*.

MISSOURI: Monteith Junction, Bates Co., *E. J. Palmer* 26069 (TYPE), Sept. 10, 1924; Butler Co., *B. F. Bush* 3770, Oct. 19, 1905; Williamsville, Wayne Co., *E. J. Palmer* 19423, Oct. 9, 1920; Cole Camp, Benton Co., *E. J. Palmer* 26358, Oct. 1, 1924.

× *Quercus neopalmeri*¹ Sudworth (*Q. nigra* × *Shumardii*), *Check List Forest Trees U. S.* 92. 1927.

Quercus nigra × *Shumardii* Palmer, *Jour. Arnold Arb.* 4: 21. 1923.

The original specimen was without fruit, and several other sterile specimens have since been found in other places.

GEORGIA: Wilkes Co., *T. G. Harbison* 15, June 15, 1919; Folkston, *T. G. Harbison* 101, Nov. 26, 1919. FLORIDA: Oviedo, *T. G. Harbison* 11, May 28, 1917; Sumner, *T. G. Harbison* 30, June 16, 1917. ARKANSAS: McNab, Hempstead Co., *E. J. Palmer* 22301 (TYPE), Oct. 12, 1922. ALABAMA: Cullman, *T. G. Harbison* 12, Nov. 4, 1919.

× *Quercus Nessiana* hybr. nov. (*Q. bicolor* × *virginiana*).

Arbor foliis tarde deciduis obovatis 5–13-lobatis vel raro incomposite pauci-lobatis vel integris maturis subcoriaciis supra fere glabratris infra dense tenuiter pubescentibus.

The hybrid between the swamp white oak and the live oak has not so far been found in the wild state. But the two species were crossed by the late Professor Helge Ness at the Experiment Station of the Texas Agricultural College, College Station, Texas.

¹ Arbor foliis ferme obovatis incomposite lobatis basi cuneatis maturis glabris venu-
lorum axillis barbatis exceptis.

Writing about some of the hybrids in cultivation, Ness stated: "From artificial pollination made April 3, 1918, we have three specimens of *Q. platanoides* (male) and *Q. virginiana* (female) in the Arboretum of the Experiment Station. They were planted in 1920. One of them produced a few acorns in 1923. This year, 1926, all bore heavy crops of acorns, although no male flowers were produced. They are very uniform in character, strongly resembling *Q. platanoides*; the only difference being that the leaves are somewhat smaller, more persistent, firmer, and the crown more densely branched than in *Q. platanoides*."

A specimen sent to the Arnold Arboretum about 1923 consists of two young branches with well developed leaves, resembling those of *Quercus bicolor* in shape and with the other characters mentioned by Ness. Recently Dr. W. S. Flory, Jr. has sent us a series of specimens and photographs showing leaves and fruit. The prevailing type of leaves on the specimens numbered 1 and 3 by Flory is much the same as on the Ness specimen. On no. 2 the leaves are much more variable, relatively narrower, some of them being irregularly lobed or toothed, and a few have blades with entire margins. The lobes and teeth are mucronate tipped, and the under surface of the blades is covered with a dense fine pale stellate pubescence similar to that of *Quercus bicolor*. The peduncled acorns resemble those of *Quercus bicolor* but are smaller and with deeper, more turbinate cups.

× *Quercus organensis* Trelease (*Q. arizonica* × *grisea*), Proc. Amer. Phil. Soc. 56: 50. 1917; Mem. Nat. Acad. Sci. 20: 16. 1924.

Quercus arizonica × *grisea* Wooton & Standley, Contrib. U. S. Nat. Herb. 19: 171. 1915.

A single tree growing with the supposed parent species and believed to be a hybrid between them was found at Van Patten's Camp in the Organ Mountains, according to Wooton and Standley. I have not seen the material.

(?) × *Quercus oviedoensis* Sargent (*Q. incana* × *myrtifolia*), Bot. Gaz. 65: 459. 1918; Man. Trees N. Amer. ed. 2, 266. 1922.—Trelease, Mem. Nat. Acad. Sci. 20: 16. 1924.

The type specimen of this came from a large shrub found near Oviedo, Seminole Co., Fla., and said to be growing with the supposed parent species. Another specimen from the same locality was described as coming from a small tree. All of the material is sterile and its identity seems rather doubtful.

FLORIDA: Oviedo, T. G. Harbison 19, 20 (TYPE), May 29, 1917.

× *Quercus paleolithicola* Trelease (*Q. ellipsoidalis* × *velutina*), Proc. Amer. Phil. Soc. 56: 50, pl. 1. 1917; Mem. Nat. Acad. Sci. 20: 16. 1924.

Forms of the black oak and of the jack oak approach each other in leaf and fruit characters and hybrids between them are somewhat obscure. The two species often grow in proximity and there is little doubt that they sometimes hybridize. The hybrids can generally be recognized by intermediate characters in the leaves and fruit. The young leaves, branchlets

and winter-buds are more pubescent than in *Quercus ellipsoidalis*, and the cups of the acorns are usually turbinate but with rather loose, pubescent scales.

WISCONSIN: Lake Geneva, C. S. Sargent, April 19, 1916; Sugar Loaf, Columbia Co., Huron H. Smith 8067, Aug. 5, 1922. INDIANA: southwest of Vistula, Elkhart Co., C. C. Deam 61589, Oct. 2, 1941, Ralph M. Kriebel 10048, Oct. 4, 1942; northwest of Shipshewana, Lagrange Co., Ralph M. Kriebel 10044, Oct. 4, 1942. IOWA: Fayette Co., Bruce Fink, 1893; Eldora, L. H. Pammel, Aug. 19, 1930.

× *Quercus pastorensis* C. H. Muller (*Q. clivicola* × *glaucocephala*), Jour. Arnold Arb. 17: 164. 1936.

MEXICO: Puerto de Pastores, southeast of Galena, Sierra Madre Oriental, C. H. & M. T. Muller, 1000, 1005, July 5, 1934, 1296 (TYPE), 1297, Aug. 2, 1934.

× *Quercus podophylla* Trelease (*Q. incana* × *velutina*), Proc. Amer. Phil. Soc. 56: 51. 1917; Mem. Nat. Acad. Sci. 20: 16. 1924.—Sargent, Man. Trees N. Amer. ed. 2, 243. 1922.

× *Quercus petiolaris* Ashe, Jour. Elisha Mitchell Sci. Soc. 11: 90. 1894. Not. *Q. petiolaris* Benthon, 1840.

Ashe gave the parentage of × *Quercus petiolaris* as *Q. cinerea* × *Q. tinctoria*? But his rather detailed description seems to substantiate the suggested parentage. It was stated that five or six trees were seen, the bark of all of them having the general aspect of *cinerea* (*incana*). The locality was not given, but, presumably, they were found in North Carolina. I have not seen any material of this hybrid.

(?) × *QUERCUS PSEUDOMARGARETTA* Trelease, Mem. Nat. Acad. Sci. 20: 16. 1924.

The parentage given by Trelease was *Quercus Margaretta* × *stellata*. The former was regarded by him as a distinct species and not as a variety of *Q. stellata* as held by Sargent and as here considered. Whatever view is taken of this, the two suggested parents approach each other so closely in leaf and fruit characters—especially in forms found in the western part of the coastal plain—that a hybrid between them would be very obscure and difficult to detect. I have not seen the type specimen (Fisher 5116, Houston, Tex.), but Trelease stated that it closely resembled *Margaretta*, and from his brief description and from what I have seen of the post-oak in the part of the country from which it came, I think it is probably identical with *Quercus stellata* var. *araniosa* Sargent.

× *Quercus Rehderi* Trelease (*Q. ilicifolia* × *velutina*), Proc. Amer. Phil. Soc. 56: 51. 1917; Trans. Nat. Acad. Sci. 20: 16. 1924.—Sargent, Man. Trees. N. Amer. ed. 2, 255. 1922.

Quercus ilicifolia × *velutina* Rehder, Rhodora 3: 133, pl. 24, fig. 1-2. 1903.

This hybrid seems to be comparatively frequent where the bear-oak and the black oak grow together. The leaves of the two species are quite different from each other in character and in the hybrids they are obviously intermediate. Most of the specimens observed in the field are shrubby, although sometimes stouter and more tree-like than is usual in *Quercus ilicifolia*.

MASSACHUSETTS: Blue Hills, near Boston, A. Rehder, Sept. 18 & 22, 1900, March 13, 1901; South Blue Hill Ave., near Boston, E. J. Palmer 20190, 20192, June 17, 1921; near Boston, Rufus N. Carr, Oct. 19, 1927; Norwood, J. G. Jack, June 25,

1904; Lynn Woods, *A. Rehder*, Oct. 3, 1903; West Peabody, *J. Robinson*, Sept. 12, 1880; Marthas Vinyard, *Sidney Harris*, May 30, 1901; Chilmark, Marthas Vinyard, *Sidney Harris*, May 30, June 12, 1902, Aug. 31, 1903. RHODE ISLAND: Slatersville, Providence Co., *E. J. Palmer* 43296, July 17, 1927. PENNSYLVANIA: Reading, Berks Co., *E. J. Palmer* 36306, Sept. 11, 1929; near White Bear, Berks Co., *David Berkheimer* 4379, Sept. 26, 1943.

(?) \times *Quercus Richteri* Baenitz; Allg. Bot. Zeitschr. 9: 85. 1903.

This name was proposed for a supposed hybrid between *Quercus borealis* (*rubra*) and *Q. palustris* and was based on a tree growing in Scheitniger Park, Breslau, Silesia. Specimens from the type tree collected and distributed by Baenitz and others are in the herbarium of the Arnold Arboretum. Croizat (18) after studying the material concluded that there was nothing to distinguish it from *Quercus coccinea* Muenchh. And on the evidence, I am inclined to agree with him that \times *Quercus Richteri* should be considered a synonym of that species. Several specimens from native trees in different parts of the United States are also in the Arboretum herbarium that suggest hybrids between the red oak and the pin-oak, but since all of them seem to be slightly questionable and since the name proposed by Baenitz is invalid, it is perhaps best to leave them unnamed for the present.

\times *Quercus Robbinsii* Trelease (*Q. coccinea* \times *ilicifolia*), Proc. Amer. Phil. Soc. 56: 51. 1917; Mem. Nat. Acad. Sci. 20: 16. 1924.—Sargent, Man. Trees N. Amer. ed. 2, 248. 1922.

Quercus coccinea \times *ilicifolia* Gray, Man. Bot., ed. 5, 454. 1867.—Robbins ex Engelmann (as *ilicifolia* \times *coccinea*), Trans. Acad. Sci. St. Louis 3: 542. 1877.

Specimens of this hybrid may be difficult to distinguish from \times *Quercus Rehderi*. The leaves and branchlets are less pubescent and the cups of the acorns are deeper.

MASSACHUSETTS: Uxbridge, *J. W. Robbins* (without date), (G); North Easton, *J. S. Ames* 1912, Sept. 17, 1917; Framingham, *A. J. Eames*, Sept. 6, 1909 (G). PENNSYLVANIA: Wilkes Barre, Luzerne Co., *E. J. Palmer* 36289, Sept. 9, 1929.

\times *Quercus Rudkini* Britton (*Q. marilandica* \times *Phellos*), Bull. Torrey Bot. Club 9: 13, pl. 10-12, fig. 3-5. 1888.—Sargent, Silva 8: 181, pl. 437. 1895; Man. Trees N. Amer. ed. 2, 259. 1922.—Trelease. Mem. Nat. Acad. Sci. 22: 16. 1924.

\times *Quercus dubia* Ashe, Jour. Elisha Mitchell Sci. Soc. 11: 93. 1894.

Trees that appear to be hybrids between the black jack oak and the willow-oak have been found widely scattered through the common range of the two species. The foliage is extremely variable and ranges between the leaf types of the two species and with some eccentric forms. In describing \times *Quercus dubia*, Ashe expressed the opinion that it was a hybrid between *Quercus coccinea* and *Q. Phellos*, although he was in doubt about it. Sargent (53) considered it a synonym of \times *Q. atlantica* Ashe, which he held to be a cross between *Q. incana* and *Q. laurifolia*. An isotype in the herbarium of the Arnold Arboretum shows it to be an anomalous form with large entire, oblong-elliptic leaves, and it appears to me to be an extreme form of \times *Quercus Rudkini*.

NEW YORK: Tottenville, Staten Island, *Arthur Hollick* 4, 5, 15, Sept. 2, 1888. NEW JERSEY: Keyport, *W. T. Davis* 146, Nov. 13, 1910; Bennett, Cape May Co.,

Bayard Long 7947, Oct. 29, 1912. DELAWARE: *Stanton, J. P. Otis*, 1920. VIRGINIA: *South Arlington, E. S. Steele*, Aug. 8, 1899. NORTH CAROLINA: *Falls of Yadkin River, Stanley Co., J. K. Small*, Aug. 18, 1893; *Blondin Co., W. W. Ashe* 247, June and Nov., 1895; *Raleigh, W. W. Ashe*, March and Oct.; *Chapel Hill, T. G. Harbison* 25, May 30, 1919; *Abbotsburg, Bladen Co., T. G. Harbison* 11, 1916, Oct. 5, 1917, *J. S. Holmes*, May 9, 1918. SOUTH CAROLINA: *Charleston, T. G. Harbison* 30, May 1, 1917. GEORGIA: *Wilkes Co., T. G. Harbison* 48, June 15, 1919. FLORIDA: *Gainesville, T. G. Harbison* 46, June 17, 1917. ARKANSAS: *Fulton, Hempstead Co., B. F. Bush* 1093, Oct. 17, 1901, 5946, Oct. 5, 1909, *E. J. Palmer* 10504, July 17, 1916, 10580, Sept. 4, 1916, 22276, Oct. 12, 1922, 22465, April 25, 23999, Oct. 4, 1923. LOUISIANA: *west of Bogalusa, Washington Parish, Clair A. Brown* 7721, June 4, 1939; *Chestnut, Natchitoches Parish, E. J. Palmer* 9471, April 17, 1916. Cultivated at Arnold Arboretum, Brooklyn Botanic Garden, and University of North Carolina. 

× *Quercus runcinata* (A. DC.) Engelmann (*Q. borealis* × *imbricaria*), *Oaks of U. S.* 20. 1876.—Sargent, *Man. Trees N. Amer.* ed. 2, 243. 1922.
Quercus rubra β *runcinata* A. de Candolle, *Prodr.* 16(2): 60. 1864.—Gray, *Man. Bot.* ed. 5, 454. 1868.

Engelmann stated that he collected the type material of this in the bottomlands of the Mississippi River opposite St. Louis, growing with *rubra*, *imbricaria*, and *palustris*. He believed it to be a hybrid between the first two, and sent a specimen under the name × *Quercus runcinata* to A. de Candolle, who regarded it as merely a form of the red oak and so published a description under the combination shown above. Engelmann in his notes (24) in which he published the name × *Quercus runcinata* for the first time expressed himself as willing to defer to Candolle's opinion. However, there can be little doubt that Engelmann's plant and numerous later discoveries are really hybrids of the parentage he first suggested.

PENNSYLVANIA: *Westmoreland Co., Henry Chisman*, 1936; *near Ambler, James R. Gilpin*, Sept. 19, 1934. MARYLAND: *Ammendale, F. S. C.*—, Oct. 13, 1928. OHIO: *near Akron, Fred H. Gleny*, 1938; *West Union, Conrad Roth*, Oct., 1931; *Columbus, W. A. Kellerman* (without date). INDIANA: *near Bedford, Ralph M. Kriebel* 2767, 2768, Oct. 1934; *near Oakland City, Gibson Co., Ralph M. Kriebel*, 1939. ILLINOIS: *near Sannon Bridge, Wayne Co., Robt. Ridgway* 91, Oct. 21, 1914; *near mouth of Turkey Creek, Richland Co., Robt. Ridgway* 26, Aug. 12, 1917; 10 miles northeast of Olney, Richland Co., *Robt. Ridgway* 2687, Sept. 19, 1926; *East St. Louis, Geo. Engelmann*, Sept. 28, 1849; *Tunnel Hill, Johnson Co., E. J. Palmer* 19579, Oct. 23, 1920; *Simpson, Johnson Co., E. J. Palmer* 16666, Oct. 4, 1919. KENTUCKY: *Sparta, Donaldson*, 1935. MISSOURI: *Allenton, St. Louis Co., G. W. Letterman* 2, 1880, 3, July, 1878, 5, May 10, 1891, 6, Nov. 1, 1891, 36 (without date), Oct. 1890; *near Independence, B. F. Bush* 623, Sept. 16, 1894, 628, Oct. 14, 1895, 10347-a, Sept. 22, 1924; *Hyde Park, Kansas City, Kendall Laughlin*, Oct., 1935; *Van Buren, Carter Co., E. J. Palmer* 19497, Oct. 11, 1920. Cultivated in the Arnold Arboretum, Bronx Park, New York, and in other parks and gardens in the United States and Europe.

× *Quercus Sargentii* Rehder (*Q. montana* × *robur*), in *Bailey Stand. Cyclop. Hort.* 5: 2886. 1916; *Mitt. Deutsh. Dendr. Ges.* 1915(24): 215. 1916.—Sargent, *Man. Trees N. Amer.* ed. 2, 306. 1922.

This hybrid between the chestnut-oak and the English oak was discovered on the grounds of Professor C. S. Sargent, Holm Lea, Brookline, Mass. Large trees are now growing in the Arnold Arboretum grown from seeds

of the original tree planted in 1877. The seedlings, although differing from each other, retain the intermediate characters of the original hybrid.

× *Quercus Saulei* Schneider (*Q. alba* × *montana*), Ill. Handb. Laubh. 1: 203. 1904.
— Sargent, Man. Trees N. Amer. ed. 2, 302. 1922.

Quercus alba × *Prinus* Engelmann, Trans. Acad. Sci. St. Louis 3: 399. 1877.—
Vasey, Bull. Torrey Bot. Club 10: 25, pl. 28-30. 1883.— Sargent, Silva 8: 18,
pl. 361. 1895.

This seems to be one of the commonest hybrids among the white oaks, and it may be looked for wherever the two parent species are found growing together. The leaves are usually symmetric and are more uniform in type than is the case with most hybrids. The blades usually resemble those of the chestnut-oak in outline, but are more deeply incised with mostly simple ovate or oblong lobes rounded at the apex.

VERMONT: Monkton, C. G. Pringle, May 21, Sept. 29, 1879. MASSACHUSETTS:
Jamaica Plain, C. E. Faxon, July 16, 1897, J. G. Jack, March 25, Sept. 21, 1914;
Concord, H. A. Purdie, Aug. 1903; Middlesex Fells, H. J. Koehler, June, 1908.
RHODE ISLAND: Providence, J. F. Collins, Oct. 2, 1892; Durfee Hill, near Chepachet,
Providence Co., E. J. Palmer 44641, Aug. 20, 1938; near Diamond Hill, Providence
Co., E. J. Palmer 46132, June 14, 1942, 47913, Aug. 11, 1946. NEW YORK:
Fort Wadsworth, Staten Island, Leon Croizat, June 15, 1937; Alley Pond Park,
New York, Leon Croizat, Sept. 15, 1936. PENNSYLVANIA: Roslyn, C. S. Sargent,
Sept. 13, 1914, J. C. Swartley S-856, Sept. 1936; Rocky Mountain Run, Franklin
Co., John C. Kase 17, 1935; near Hatboro, Charles C. Mann; Bedford Co., David
Berkheimer 5417, Aug. 16, 1944. NEW JERSEY: Elwood, Isaac C. Martindale, Aug.,
1877; near Newark, Hans J. Koehler, July, 1906; Sandboro, C. S. Sargent, Aug. 22,
1916; Ocean Grove, J. K. Hayward, 1890. DISTRICT OF COLUMBIA: Washington,
John Saul, May (and autumn), 1894, Geo. B. Vasey (without date); Woodley Park,
L. F. Ward, Oct. 19, 1884. NORTH CAROLINA: Biltmore, ex Herb. Biltmore, no.
5723-b, May 10, Oct. 13, 1897; Highlands, T. G. Harbison 26, May 18, 1916, 38,
Sept. 24, 1916. OHIO: Steece, F. W. Dean, July 13, 1921. KENTUCKY: Echols,
Ohio Co., E. J. Palmer 22542, May 6, 23699, Sept. 13, 1923. ALABAMA: Valleyhead,
T. G. Harbison 37, June 26, 1918. Cultivated in the Arnold Arboretum and in
Franklin Park, Boston, Mass.

× *Quercus Schochiana*¹ Dieck (*Q. palustris* × *Phellos*), Nat. Arboretums Zoschen
1894-95.— Schoch. Mitt. Deutsch. Dendr. Ges. 1896, 9.— Rehder, Man. Cult.
Trees and Shrubs ed. 2, 156. 1940.

Quercus palustris × *Phellos* Palmer, Jour. Arnold Arb. 2: 143. 1921.

This hybrid was first recognized in the park at Wörlitz, Germany, where it had appeared spontaneously. The name was first published without other description than citation of the supposed parents in a seed list by Dieck, and Schoch had a brief reference to it the following year, as cited above. It has been cultivated in several European gardens, but both the name and the hybrid plants that have lately been found native in several localities in the United States seem to have generally been overlooked by American botanists. Earlier specimens have in some cases been confused with × *Quercus heterophylla*. The leaves are quite variable, but usually resemble more closely those of the willow-oak in size and

¹ Arbor foliis lanceolatis vel oblongo-lanceolatis margine raro integris plerumque
undulatis vel incompositae acute lobatis, junioribus infra pubescentibus mox glabris
venularum axillis exceptis.

outline. The blades are mostly two to four times as long as wide, from narrowly lanceolate and entire to undulate or lobed with small asymmetric rounded or sharp bristle-tipped lobes, thinly pubescent beneath as they unfold, but soon becoming glabrous except for tufts of tomentum in the axils of the principal veins.

ILLINOIS: Cairo, Alexander Co., *E. J. Palmer* 14919, April 23, 1919, 15090, May 8, 1919, 16475, Sept. 18, 1919, 19551, Oct. 16, 1920, 29648, Nov. 16, 1925; Mounds, Pulaski Co., *E. J. Palmer* 14995, April 30, 1919; Mound City, Pulaski Co., *E. J. Palmer* 15102, May 11, 1919, 16635, Oct. 1, 1919; Olive Branch, Alexander Co. *E. J. Palmer* 15097, May 10, 1919; Brookport, Massac Co., *E. J. Palmer* 15339, June 2, 1919. KENTUCKY: Wickliff, Ballard Co., *E. J. Palmer* 15108, May 12, 1919, 16506, Sept. 20, 1919. ARKANSAS: Dover, Pope Co., *E. J. Palmer* 27096. Cultivated in the Arnold Arboretum and elsewhere in the U. S., Germany, and France.

× *Quercus Smallii* Trelease (*Q. georgiana* × *marilandica*), Proc. Amer. Phil. Soc. 56: 51. 1917; Mem. Nat. Acad. Sci. 20: 17. 1924.—Sargent, Man. Trees N. Amer. ed. 2, 250. 1922.

Quercus georgiana × *nigra* (*marilandica*), Small, Bull. Torrey Bot. Club 22: 75, pl. 233. 1895.

The leaves of the specimens examined somewhat resemble those of *Quercus marilandica* in shape, but are of thinner texture. Small's figures show leaves of a variety of shapes, some of them deeply divided and suggestive of *Q. georgiana*.

GEORGIA: Stone Mountain, De Kalb Co., *J. K. Small*, Sept. 6–12, 1894; Little Stone Mountain, De Kalb Co., *J. K. Small*, Sept. 11, 1894.

× *Quercus stelloides* Palmer (*Q. prinoides* × *stellata*), Jour. Arnold Arb. 18: 139. 1937.

The leaves of the parent species are quite different from each other and the hybrid is well-marked in its intermediate characters. The plants are usually shrubby, from one to two meters tall, but rarely they become arborescent and up to four meters or more. The leaf patterns vary between those of the parent species, but usually they resemble more closely those of *Quercus stellata*, being obovate in outline, with 3–4 pairs of shallow rounded or pointed lateral lobes, simple or rarely enlarged and indented at the apex. At maturity they are green and nearly glabrous above and pale stellate-pubescent beneath.

MASSACHUSETTS: Yarmouth, *M. L. Fernald & Bayard Long* 9360, Sept. 19, 1913; Oak Bluffs, Marthas Vineyard, *E. J. Palmer* 45188, July 4, 1940. NEW JERSEY: Hampton Furnace, Burlington Co., *J. W. Adams* 4018, Sept. 16, 1937; Newtonville, *J. W. Adams* 4076, Sept. 24, 1937; Cape May, *C. F. Austin*, 1899 (G). MISSOURI: Greenwood (Jackson Co.), *B. F. Bush* 9744, Oct. 17, 1921, 10227-a, Oct. 3, 1923, 10330, Sept. 5, 1924, *E. J. Palmer* 26032, Sept. 5, 1924. KANSAS: Neodesha, Wilson Co., *E. J. Palmer* 21398, May 23, 1922, 22007 (TYPE), Sept. 18, 1922, 24372, Oct. 31, 1923. OKLAHOMA: Muskogee, *E. J. Palmer* 14285, June 30, 1918.

× *Quercus sterilis* Trelease¹ (*Q. marilandica* × *nigra*), Proc. Amer. Phil. Soc. 56: 51. 1917.—Sargent, Man. Trees N. Amer. ed. 2, 259. 1922.

Quercus aquatica (*nigra*) × *nigra* (*marilandica*) Ashe, Jour. Elisha Mitchell Sci. Soc. 11: 92. 1894.

¹ Arbor foliis obovatis vel oblongo-obovatis integris vel ad apicem 3–5-lobatis mucronatis subsessilibus supra glabris infra aliquantum pubescentibus; venuis conspicuus. Fructus ovatus; cupula obconica squamis laxis puberulis.

Ashe's description of the tree and specimen on which the name was based was fairly adequate. Trelease in the American Oaks reduced it to synonymy under *Quercus arkansana* which he considered a hybrid of the same parentage. While the leaves of the hybrid and those of *Q. arkansana* are somewhat similar in shape in certain forms, the resemblance is superficial, those of the hybrid differing in their firmer texture and more prominent veins, in the sessile or nearly sessile base, and in the character of the pubescence. Careful study of *Quercus arkansana* in the field and in cultivation at the Arnold Arboretum leaves no room for doubt that it is a good species and not a hybrid.

NORTH CAROLINA: Bladen Co., *W. W. Ashe* 246, June 10, and Nov., 1898. GEORGIA: Climax, *T. G. Harbison* 12, Nov. 6, 1917. TEXAS: Fletcher, Hardin Co., *E. J. Palmer* 9556, April 25, 1916, 10677, Sept. 10, 1916, 12730, Sept. 13, 1917, 13103, March 17, 1918.

× *Quercus Sterrettii* Trelease (*Q. lyrata* × *stellata*), *Mem. Nat. Acad. Sci.* 20: 17. 1924.

This hybrid may be recognized by the shape of the leaves, which are loosely stellate-pubescent beneath and with traces of pubescence at least along the midrib above at maturity. I have not seen the specimen on which the description was based (*W. D. Sterrett*, no. 6, July 28, 1917, Little Rock, Ark.). Presumably, it was sterile, as no mention was made of the fruit. But on the specimen cited below the immature fruit is peduncled and resembles that of the overcup oak.

ARKANSAS: between Brinkley and Wheatley, Monroe Co., *Delzie Demaree* 10883, Aug. 30, 1934.

× *Quercus subintegra* (Engelm.) Trelease (*Q. incana* × *falcata*), *Proc. Amer. Phil. Soc.* 56: 52. 1917; *Mem. Nat. Acad. Sci.* 20: 17. 1924.—Sargent, *Man. Trees N. Amer.* ed. 2, 266. 1922.

Quercus falcata var. *subintegra* Engelmann, *Trans. Acad. Sci. St. Louis* 3: 542. 1877.

The original specimen of this hybrid was collected by J. H. Mellichamp near Bluffton, South Carolina, and sent to Engelmann, who believed it to be a hybrid between *Quercus cinerea* (*incana*) and *Q. falcata*. It was first mentioned and described under the name *Q. falcato-cinerea* in the Oaks of the United States, a preprint of the Transactions of the Academy of Science of St. Louis for 1876, and in pages that were later "cancelled" by the author. Engelmann later decided that it was only a variety of *Quercus falcata*, but his first surmise seems to have been the correct one. I have not seen the type specimen, but several later collections listed below appear to belong with it.

GEORGIA: Lumber City, *T. G. Harbison* 5, May 30, 1917, 18, Nov. 10, 1917; Climax, *T. G. Harbison* 2, May 29, 1917; Decatur, *T. G. Harbison* 22, June 21, 1917; Traders Hill, *T. G. Harbison* 7, April 3, 1918. FLORIDA: Lake City, *T. G. Harbison* 22, June 23, 1917; Ocala, Marion Co., *E. J. Palmer* 38304, March 31, 1931. ALABAMA: Mobile, *T. G. Harbison* 4, Dec. 4, 1919.

× *Quercus sublaurifolia* Trelease¹ (*Q. incana* × *laurifolia*), *Proc. Amer. Phil. Soc.* 56: 52. 1917.—Sargent, *Man. Trees N. Amer.* ed. 2, 266. 1922.

Quercus cinerea × *laurifolia* Ashe, *Jour. Elisha Mitchell Sci. Soc.* 11: 89. 1894.

¹ *Arbor minor* foliis lanceolatis integris vel raro oblongo-ovovatis inaequaliter lobatis apice mucronatis maturis subcoriaceis subtus pallidis pubescentibus.

No description or citation of specimens accompanied the publication of this name, but it was doubtless based on Ashe's collection and the publication referred to above, in which a good English description was given. In the American Oaks Trelease reduced it to synonymy under *× Quercus atlantica*. See discussion under that name. A number of specimens that apparently represent this hybrid were found in the herbarium of the Arnold Arboretum under the name *× Quercus dubia* Ashe, as interpreted by Sargent. Some of them are of doubtful relationship and can be distinguished from *Q. laurifolia* only by the presence of stellate pubescence on the mature leaves: others are possibly of a different hybrid origin.

SOUTH CAROLINA: Port Royal, *T. G. Harbison* 16, 17, Dec. 9, 1917; St. Helens Island, *T. G. Harbison* 1, 2, Oct. 27, 1917. GEORGIA: Lumber City, *T. G. Harbison* 5, 8, Dec. 15, 1917, 16, Dec. 16, 1917; Folkston, *T. G. Harbison* 26, May 15, 1918, 51, 53, May 16, 1918. FLORIDA: San Mateo, *T. G. Harbison* 1, 2, 13, May 26, 1917, 20, 22, 26, 27, 28, Dec. 12, 1917; Orlando, *T. G. Harbison* 20, 21, 25, Dec. 5, 1917, 38, Dec. 14, 1919; Plymouth, *T. G. Harbison* 35, Nov. 13, 1919. ALABAMA: Mt. Vernon, *T. G. Harbison* 11, Nov. 19, 1917.

× *Quercus substellata* Trelease (*Q. bicolor* × *stellata*), *Mem. Nat. Acad. Sci.* 20: 17. 1924.

I have not seen any material representing this hybrid. According to the description, it was based on a specimen collected by Percy Wilson, at Toms River, N. J., July, 1916.

× *Quercus Townei* hybr. nov. (*Q. dumosa* × *lobata*).

Arbor vel arbuscula ad 5–6 m. alta, ramulis gracilibus annotinis cinereo-viridibus vel brunneis tomentosis lenticulis pallidis conspicuis. Folia persistentia oblonga vel anguste obovata basi cuneata vel rotunda, margine revoluto leviter vel profunde incisa lobis rotundis vel acutis mucronatis subtus sparse stellato-pubescentia. Fructus annuus oblongo-ovatus; glans 2–3.5 cm. longa; cupula hemispherica squamis valde crassis pubescentibus.

Two trees supposed to be this hybrid were found by Mr. Stuart S. Towne, for whom it is named, near Pasadena, California, and a series of specimens with notes was sent by him to Professor C. S. Sargent. The notes stated that *Quercus dumosa* is abundant and extremely variable on the hills in the vicinity of the hybrid, but that *Q. lobata* is not known nearer than about four miles away. The leaves of the hybrid have more resemblance to those of *Quercus lobata* than to those of the other parent, but they are smaller, relatively narrower, and less deeply incised. The acorns are also somewhat intermediate between the two species, with the nut shorter and less pointed than that of *Quercus lobata*.

CALIFORNIA: near Pasadena along La Loma Road, *Stuart S. Towne* 1, 2, Sept. 23, 1918, (autumn), 1921, 1922.

× *Quercus tridentata* (A. DC.) Engelmann (*Q. imbricaria* × *marilandica*), *Oaks of U. S.* 18, 1876; *Trans. Acad. Sci. St. Louis* 3: 539. 1877.—Sargent, *Man. Trees N. Amer.* ed. 2, 268. 1922.

Engelmann stated that a single tree of this hybrid was found by him in the autumn of 1849, about six miles east of St. Louis, growing in company with the supposed parents. He remarked that the foliage and fruit

characters were such that the origin of the hybrid could scarcely be doubted, that the leaves were rather those of *imbricaria* with a touch of *nigra (marilandica)*, and that the fruit was more like that of *nigra*. The hybrid is apparently an uncommon one, but specimens that probably belong with it have been found elsewhere within the common range of the parent species. A number of other specimens have been referred to it on account of their somewhat similar leaves with three-lobed apex, but in most cases they appear to belong with either \times *Quercus runcinata*, \times *Q. heterophylla* or \times *Q. Leana*.

ILLINOIS: Richland Co., *Robt. Ridgway* 90, Oct. 1914, 2810, May 28, 1927; Olney, *Robt. Ridgway*, Feb., 1917, *E. J. Palmer* 15584, June 24, 1919. MISSOURI: Cape Girardeau, *E. J. Palmer* 18012, June 22, 1920.

\times *Quercus vaga* Palmer & Steyermark (*Q. palustris* \times *velutina*), *Ann. Missouri Bot. Gard.* 22: 521. 1935.

Only a single tree of this hybrid is known, and it was found growing with the supposed parent species. The bark and habit resemble *Quercus palustris*, and the leaves are also of the *palustris* type and retain the characteristic tufts of tomentum in the axils of the veins. Traces of easily detached tomentum remain on the young branchlets and on the under surface of the leaves until mid-summer. The scales on the cups of the young acorns are loosely imbricated and pubescent, as in *Quercus velutina*.

MISSOURI: Maryville, *E. J. Palmer* 25421, June 13, 1924.

\times *QUERCUS VENULOSA* Ashe, *Jour. Elisha Mitchell Sci. Soc.* 41: 268. 1926.

This name was proposed by Ashe for what he believed to be a hybrid between *Quercus caput-rivuli* and *Q. cinerea (incana)*. But the former has been reduced to a variety of *Quercus arkansana* (Ashe, *Jour. Elisha Mitchell Sci. Soc.* 40: 44. 1924). And Little (33) has pointed out that the name cannot be retained because it is a later homonym of a fossil species, and he prudently suggested that the supposed hybrid should receive further study before it is renamed. An isotype (*W. W. Ashe*, no. 217, Okaloosa Co., Fla., Nov., 1924) in the herbarium of the Arnold Arboretum shows mature leaves, branchlets, and winter-buds. There can be little doubt of its relationship with *Quercus arkansana* or its variety, but I think there might easily be a question as to the other parent species. There is little except the slightly narrower entire leaves to suggest *Quercus incana*, and it is possible that *Q. obtusa* may have been the other parent.

\times *Quercus Walteriana* Ashe (*Q. laevis* \times *nigra*), *Proc. Soc. Amer. Foresters* 11: 89. 1916.—Sargent, *Man. Trees N. Amer.* ed. 2, 254. 1922.

\times *Quercus sinuata* Engelmann, *Trans. Acad. Sci. St. Louis* 3: 400. 1877.—Sargent, *Silva* 8: 144, pl. 418. 1895. *Not. Q. sinuata* Walt.?

In proposing this name Ashe called attention to the fact that Engelmann, followed by Sargent, had referred this hybrid to *Quercus sinuata* Walt., which he believed to be the white oak later described by Small as *Quercus austrina*. However, from the brief description given by Walter it does not seem possible to determine the identity of *Q. sinuata*, although it was

probably a hybrid and could scarcely have been *Q. austrina*.¹ So it seems best under the circumstances to accept Ashe's name.

SOUTH CAROLINA: Bluffton, *J. H. Mellichamp*, 1884, May 2, 1890, June, 1894, *C. S. Sargent*, Oct. 4, 1894, *T. G. Harbison* 14, Aug. 29, 1916; Walhalla, *T. G. Harbison* 10, Oct. 11, 1917. GEORGIA: Lumber City, *T. G. Harbison* 17, Nov. 16, 1917. FLORIDA: Jacksonville, *T. G. Harbison* 18, Dec. 3, 1917.

× *Quercus Willdenowiana* (Dippel) Zabel (*Q. falcata* × *velutina*), in Beissner, Schelle and Zabel, Laubh.-Ben. 67, 1903.—Schneider, Ill. Handb. Laubh. 1: 171, 1897.—Sargent, Man. Trees N. Amer. ed. 2, 257, 1922.

Quercus tinctoria Willdenowiana Dippel, Handb. Laubh. 2: 122, 1922.

× *Quercus Sudworthi* Trelease, Proc. Amer. Phil. Soc. 56: 52, 1917.

This hybrid was described from plants cultivated in Europe, and I have not seen the original material. But plants that apparently belong with it have been found in several parts of the United States.

NORTH CAROLINA: Biltmore, ex Herb. Biltmore, no. 5723-d, Sept. 20, 1897.

GEORGIA: Cornelia, *T. G. Harbison* 24, June 30, 1918, 46, Oct. 1, 1919. ARKANSAS: Ozark, *Albert Ruth* 96, Sept. 14, 1927.

In addition to the hybrids enumerated and discussed in this list several others are indicated by material in the herbarium of the Arnold Arboretum and other collections. Among these are *Quercus alba* × *lyrata*, *Q. bicolor* × *montana*, *Q. bicolor* × *robur*, *Q. borealis* × *ellipsoidalis*, *Q. borealis* × *marilandica*, *Q. coccinea* × *palustris*, *Q. Durandii (austrina)* × *lyrata*, *Q. Durandii (austrina)* × *virginiana*, *Q. falcata* × *marilandica*, *Q. falcata* × *nigra*, *Q. hypoleucoides* × *Shumardii (texana)*, *Q. incana* × *Phellos*, *Q. laevis* × *nigra*, *Q. macrocarpa* × *robur*, *Q. Nuttallii* × *Shumardii*, and others. There is no doubt that most of the specimens are from plants of hybrid origin and in some cases they are more complete and convincing than the types of some of the hybrids that have already been named. But since most of the specimens are without fruit and in nearly all cases there may be room for doubt as to the identity of one of the parents, it seems best to wait for fuller material or for further field study before naming them.

The hybrid oaks afford an interesting field for investigation and the subject is one that is worthy of much more attention. The present paper purports to do little more than to review the subject and to bring together the information already available in a convenient form for study. Many questions of identity and in regard to the variability and the behavior of the different hybrids will not be cleared up until they are approached experimentally and with the aid of cytological study.

¹ See Palmer, Amer. Midl. Nat. 33: 518, 1945.

BIBLIOGRAPHY

1. ALEXANDER, S. Some interesting Michigan plants; possibly some new species. *Rept. Mich. Acad. Sci.* 6: 88-89. 1904.
2. ALLARD, H. A. A progeny study of the so-called species *Quercus Saulei*, with notes on other probable hybrids found in or near the District of Columbia. *Bull. Torrey Bot. Club* 59: 267-255, fig. 1-4. 1932.
3. ———. The hybrid oak, *Quercus Rudkini*, at Arlington, Virginia. *Rhodora* 44: 262-266, pl. 709. 1942.
4. ASHE, W. W. A new post oak and hybrid oaks. *Jour. Elisha Mitchell Sci. Soc.* 11: 87-95. 1894.
5. ———. Notes on trees. *Proc. Soc. Amer. Foresters* 11: 88-90. 1916.
6. ———. Notes on trees and shrubs of the southeastern United States. *Bull. Torrey Bot. Club* 49: 268. 1922.
7. ———. Notes on woody plants. *Jour. Elisha Mitchell Sci. Soc.* 41: 267-269. 1926.
8. BAENTZ, CARL G. Die Nordamerikanischen scharlach-Eichen und ihre Bastarde in den Scheitniger Anlagen in Breslau. *Allg. Bot.* 9: 81-87. 1903.
9. BRAUN, A. (Notes on *Quercus imbricaria* \times *palustris*). *Sitzungsber. Gesellsch. Naturf. Freunde*, Dec. 20, 1870; *Bot. Zeit.* 29: 202-203, 1871.
10. BRITTON, N. L. On a hybrid oak near Keyport, N. J. *Bull. Torrey Bot. Club* 9:13-14. 1882.
11. ———. & J. A. SHAFER. North American Trees (*Quercus* 276-343). 1908.
12. BUCKLEY, S. B. Notes on the Bartram oak. *Proc. Acad. Nat. Sci. Phila.* 1861: 361. 1861.
13. BUSH, B. F. Hybrid oaks in western Missouri. *Garden and Forest* 8: 32-33. 1895.
14. ———. *Quercus Phellos* \times *rubra* in Missouri. *Garden and Forest* 8: 379. 1895.
15. ———. A list of the trees, shrubs and vines of Missouri. *Missouri Hort. Soc. Rept.* June, 1895 (*Quercus* p. 362-367).
16. CAMUS, A. *Les Chênes*, *Encycl. Econ. Sylvicult.* vol. 6-7; *Atlas* 1-2: 1934-1939.
17. CANDOLLE, A. DE. *Prodromus* 16(2): 60-79. 1864.
18. CROIZAT, LEON. An interesting oak in New York City with brief notes on *Quercus Richteri* Baen. *Torreya* 36: 141-142. 1936.
19. DANIELS, FRANCIS. Flora of Columbia, Missouri, and vicinity. *Univ. Missouri Studies Sci. Ser.* 1, 1-319 (*Quercus* p. 123-125). 1907.
20. DAVIS, WILLIAM T. A new hybrid oak. *Scientific American*, Sept. 3, 1892.
21. ———. Interesting oaks recently discovered on Staten Island. *Bull. Torrey Bot. Club* 19: 301-303. 1892.
22. DEAM, C. C. Trees of Indiana. *Rep. Indiana Board Forestry*, *Bull.* 2: 127, pl. 44 (*Quercus alba* \times *Muhlenbergii*). 1912.
23. ———. Flora of Indiana (*Quercus* p. 379-390. 1940).
24. ENGELMANN, GEORGE. The oaks of the United States. 1876 (preprint); *Trans. Acad. Sci. St. Louis* 3: 539-543. 1877.
25. FLORY, W. S., JR. & F. R. BRISON. Propagation of a rapid growing semi-evergreen oak. *Texas Agric. Exper. Sta. Bull.* 612: fig. 1-11. 1942.
26. GALE, L. D. On the oaks of the District of Columbia. *Proc. Nat. Inst. Distr. Columbia* 1: 67-77, fig. 1-2. 1856.
27. GREENE, E. L. West American oaks, pages 3 and 79, pl. 2. 1889.
28. HITCHCOCK, A. S. Another hybrid oak. *Bot. Gaz.* 18: 110-111, pl. 8. 1893.

29. HOLICK, ARTHUR. A recent discovery of hybrid oaks on Staten Island. *Bull. Torrey Bot. Club* 15: 303-309, pl. 83-85. 1888.
30. HOUBA, J. *Les Chênes de L'Amerique en Belgique*. 1887.
31. KELLOGG, ALBERT K. *Proc. California Acad. Sci.* Nov. 30, 1859, 2: 36. 1863.
32. KNOWLTON, C. H. & WALTER DEAN. *Rept. Flora Boston Distr.* 19. *Rhodora* 16: (Quercus p. 112-113). 1914.
33. LITTLE, E. L., JR. New names in *Quercus* and *Osmanthus*. *Jour. Washington Acad. Sci.* 33: 8-11. 1943.
34. MACDOUGALL, D. T. Hybridization in wild plants. *Bot. Gaz.* 43: 45-48, fig. 1-4. 1907.
35. MARTINDALE, ISAAC C. Notes on the Bartram oak, Camden, N. J. 1880.
36. MICHaux, F. ANDRÉ. *Histoire des arbres forestiers de L'Amerique Septentrionale* 2: (Quercus 1-128, pl. 1-26). 1812; *North American Silva* (English ed., translated by A. L. Hillhouse) 1: (Quercus 9-112, pl. 1-28). 1819.
37. MULLER, C. H. Studies in the oaks of the mountains of northeastern Mexico. *Jour. Arnold Arb.* 17: 160-170. 1936.
38. —. Further studies in the southwestern oaks. *Amer. Midl. Naturalist* 19: 582-588. 1938.
39. NESS, HELGE. Hybrids of the live oak and overcup oak. *Jour. Heredity* 9: 263-268, fig. 6-8. 1918.
40. —. Possibilities of hybrid oaks. *Jour. Heredity* 18: 381-386, fig. 2-3. 1927.
41. NUTTALL, THOMAS. *Silva of North America* 1: (Quercus p. 6-23, pl. 1-5). 1919.
42. PALMER, ERNEST J. The Red River forest at Fulton, Arkansas. *Jour. Arnold Arb.* 4: (Quercus p. 20-21). 1923.
43. —. Is *Quercus arkansana* a hybrid? *Jour. Arnold Arb.* 6: 195-200. 1925.
44. —. The Ligneous flora of Hot Springs National Park and vicinity. *Jour. Arnold Arb.* 7: (Quercus p. 118-120). 1926.
45. —. Notes on North American trees and shrubs. *Jour. Arnold Arb.* 18: 139-140. 1937.
46. — & JULIAN A. STEYERMARK. An annotated catalogue of the flowering plants of Missouri. *Ann. Missouri Bot. Gard.* 22: (Quercus p. 517-521). 1935.
47. REHDER, ALFRED. Notes on hybrids of *Quercus ilexifolia*. *Rhodora* 3: 137-140, pl. 24. 1901.
48. —. Neue oder Kritische gehölze. *Mitt. Deutsche Dendr.* 1915, Ges., 215. 1916.
49. —. New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum. *Jour. Arnold Arb.* 7: 239-240. 1926.
50. —. Manual of cultivated trees and shrubs, ed. 2: (Quercus p. 153-174). 1940.
51. SARGENT, C. S. *Silva of North America* 8: 1-185, pl. 356-438. 1895.
52. —. (*Quercus ludoviciana* n. hyb.). *Trees and Shrubs* 2: 223. 1913.
53. —. Notes on North American trees, 1, *Quercus*. *Bot. Gaz.* 65: 450-459. 1918.
54. —. Manual of the trees of North America, ed. 2 (Quercus p. 237-308, fig. 221-281). 1922.
55. SCHNEIDER, C. K. *Illustriertes Handbuch der Laubholzkunde* 1: (Quercus p. 161-211, fig. 97-133). 1908.
56. SCHREINER, E. J. & JOHN W. DUFFIELD. Metaxia in an oak species cross. *Jour. Heredity* 33: 97-98, fig. 5. 1942.
57. SHIMEK, B. A hybrid oak. *Proc. Iowa Acad. Sci.* 15: 77-82, pl. 1-3. 1893.

58. SMALL, J. K. Some new hybrid oaks from the southern states. Bull. Torrey Bot. Club 22: 74-76, pl. 233-235. 1895.
59. ———. Manual of the Southeastern flora. (Quercus p. 421-431). 1933.
60. SUDWORTH, GEORGE B. Nomenclature of the arborecent flora of the United States. Div. of Forestry, U. S. Dept. Agric., Bull. 14 (Quercus p. 151-179). 1897.
61. ———. Forest trees of the Pacific slope, 311-312, fig. 144. 1908.
62. ———. Hybrid oaks. Amer. Forestry 23: 683-685, fig. 1-5. 1917.
- 63: ———. Check list of the forest trees of the United States. U. S. Dept. Agric. Misc. Circular 92 (Quercus p. 83-111). 1927.
64. TRELEASE, WILLIAM. Naming American hybrid oaks. Proc. Amer. Phil. Soc. 56(no. 1): 44-52, pl. 1-3. 1917.
65. ———. The American oaks. Mem. Nat. Acad. Sci. 20: pp. 255, pl. 1-420. 1924.
66. VASEY, GEORGE B. On three hybrid oaks near Washington, D. C. Bull. Torrey Bot. Club 10: 25-26, pl. 28-30. 1883.
67. WARD, LESTER F. Oaks of the Potomac side. Field and Forest 1: 39-42. 1875.
68. WOLF, CARL B. The Gander oak, a new hybrid oak from San Diego County, California. Proc. Calif. Acad. Sci., ser. 4, 25: 177-187, pl. 19-20. 1944.
69. WOLF, W. Quercus bernardensis sp. nov. Torreya 18: 161-162. 1918.
70. ———. Quercus Capesii (Quercus Phellos L. \times Quercus nigra L.). Castanea 10: 91, 120. 1945.
71. WOOTON, E. O. & P. C. STANDLEY. Flora of New Mexico. Contrib. U. S. Nat. Herb. 19: (Quercus p. 164-174). 1915.
72. YARNELL, S. H. Inheritance in an oak species hybrid. Jour. Arnold Arb. 14: 68-75, fig. 1-8. 1933.

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A TAXONOMIC REVISION OF PODOCARPUS

I. THE SECTIONS OF THE GENUS AND THEIR SUBDIVISIONS
WITH SPECIAL REFERENCE TO LEAF ANATOMY

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THIS STUDY of the genus *Podocarpus* stems from a preliminary examination of leaf anatomy. The accounts of Bertrand (1) and Mahlert (10) have yielded conflicting data which seem, after examination of numerous specimens, to be due to the use of material by earlier investigators that had been erroneously identified and to the meagre number of specimens available. With certain corrections, the work of Mahlert (10) appears to furnish a fairly consistent key to the limited number of species considered. Therefore, we began to apply these keys, as corrected, to the species more recently described. We were also inspired by the detailed work of Florin (5) which is confined almost entirely to cuticular anatomy and it seemed that this, in combination with the entire leaf structure, might contribute to a much more accurate classification of species.

Immediately the problem of correctly identifying the specimens found in American collections became a necessity. We have been successful in locating types, isotypes, topotypes and other authentic material of nearly all American species. These provided a sound basis for the comparison of the large number of specimens we had available. All other taxonomic characters shown by the specimens were studied as well and thus it has been possible to render more nearly complete descriptions for many species as well as descriptions of numerous new species and varieties. Hence we are combining the results of our researches on leaf anatomy with the form of presentation used in taxonomic monographs. There is still the shortcoming of having our studies based too largely upon specimens found in American collections, but we have in many instances secured leaf specimens from types and isotypes in European collections and other critically authenticated material, and are therefore enabled to extend our studies and treatment provisionally to collections found in all parts of the world.

A detailed study of leaf anatomy of *Podocarpus* from specimens found in English and Scottish herbaria was made by Orr (11) to determine the value, if any, of these characters in the identification of species. In general our results are in agreement. Unfortunately, in cases of difference, we cannot correlate Orr's work with ours as he does not list the specimens which he examined, and we found the percentage of erroneously named specimens in all herbaria to be extremely high.

Keys based upon leaf anatomy alone lead to all the sections of this large genus. A few individual species may be singled out through leaf anatomy and groups within the sections may also often be recognized by this method. The remaining bulk of the species, then, must ultimately be separated by the usual taxonomic comparison of leaf size and shape, midrib and surface, bud scales, and finally the all-important reproductive characters. Whereas Pilger's keys (12) require a knowledge of reproductive structures at the beginning of analysis of most groups of species, our keys require these details only toward the end of this procedure or in the final determination of species. We feel convinced that our keys to sections and groups of species within sections are very useful due to the abundance of sterile material, and that some of these leaf characters are as important in the definition of sections as the reproductive features which originally formed the entire basis of classification.

DESCRIPTION OF LEAF ANATOMY OF *PODOCARPUS*

The constancy of internal leaf characters must be demonstrated in the same manner as external characters before they can be used in the determination of groups or species. In using herbarium specimens it must be recognized that methods of collecting and preparing the specimens will alter the color of the leaves, appearance of veins and margins, etc. Mature leaves of the coriaceous type with sufficient sclerids to reinforce the tissues will show a more true character than thin or immature leaves with undeveloped sclerids and cuticle. The internal anatomy of a leaf, easily observed in *Podocarpus* in leaf cross sections, is not changed by collecting methods except in the degree of crushing. But in no case has a thorough study been made of geographical influences on *Podocarpus* and only one or two species (Griffith 8) have been studied in detail in relation to the age of the leaves or the age of the tree or shrub from which the collections were made. Here reference must be made to work on other conifer leaves. An excellent example of such a study is that made by Fulling (7) in *Abies*, and his analysis showed no structural deviations in anatomical features due to sunny or shady portions of a tree, upper or lower portions of a tree, and no correlation with environment. There was only slight variation in positions of resin canals and thickness of hypodermal cell walls, and greater variation in the continuity and abundance of hypoderm. In herbarium specimens he found that the character of the midrib, if at all variable, was practically useless.

A thorough study of leaves from every herbarium specimen of *Podocarpus* available has shown the degree of variation within the species to be small. It has also shown that a single character, such as a large number of vascular sclerids, may be a consistent and distinguishing character in one species or group, while in another species or group it is a character of considerable variation. An analysis of useful anatomical and some external characters follows.

Size of leaf: When a description is based on a single specimen, the variation allowed in the leaves may be entirely inadequate for identification of further specimens. In general, leaves on fruiting branches are smaller, often by half, than other foliage leaves. Extremely large leaves have been collected from seedlings and vigorous shoots of most species.

Midvein: The character of the midvein — prominent or impressed — has been used by taxonomists in species descriptions as a means of differentiation and this procedure has been followed by those identifying herbarium specimens. After careful examination of many leaves in cross section it has been found that it is most valuable when leaves are mature and coriaceous or contain abundant sclerenchyma. The very strict selection of sulcate or prominently ribbed leaves has led to errors in identification in species where it is a variable character, and a number of errors have been made by ignoring the character entirely.

Vascular bundle: The shape is often characteristic in the sections, but little difference among species within the sections has been observed. Figs. 1-5 showing leaf sections include extremes in bundle size and shape.

Transfusion tissue: Transfusion tissue is located on each side of the vascular bundle in a wing formation. It may be a small area (figs. 1 & 7) in sections *Dacrycarpus* and *Stachycarpus*, larger and clear in sections *Sundacarpus* (fig. 2) and *Eupodocarpus* or extend halfway into the blade of the leaf in sections *Afrocarpus* (fig. 3) and *Polypodiopsis* (fig. 4).

Resin canals: Basically there is always one resin canal directly below the vascular bundle. In sections *Sundacarpus*, *Afrocarpus*, *Polypodiopsis* and *Eupodocarpus* (African) it may be flanked by an additional canal on each side. Always in African *Eupodocarpus* (fig. 5) and often in *P. Rospigliosii* (*Polypodiopsis*) there are also resin canals in the extreme margins of the leaves. A special deviation from this pattern will be described under *P. Rospigliosii*.

Accessory transfusion tissue: This tissue has often been described in the literature as, among the Coniferae, it is peculiar to certain sections of *Podocarpus*. It consists of pitted sclerids arranged perpendicular to the vascular bundle in a layer varying in thickness and degree of thickening, extending from each side of the transfusion tissue into the margin of the leaf. This tissue may be entirely absent or replaced by isolated sclerids. Figures 2, 3, 5, 8 and 9 show accessory transfusion tissue. The nature of this tissue has been ably discussed by Worsdell (16) and Orr (11).

Hypoderm: Many previous workers have endeavored to use the size of hypodermal cells, thickness of walls, size of cell lumen, continuity of the layer, number of layers, and length of interruptions in the layers as differentiating characters. We also recognize and use the appearance of the hypoderm, but great care must be observed to state its limitations as many species show it to be variable in one way or another instead of being constant. We believe that variation, when limits are stated, does not detract from its use in identification. Hypoderm may be seen in figs. 1, 3, 4, 5, 8, 9 and 10.

Sclerids: We now refer to types of sclerids present in the leaves other than those already described as forming distinct tissues.

a. **VASCULAR SCLERIDS:** Associated with the vascular bundle there are often long fibres with thick walls and almost no lumen. Measurements have shown these to be over a millimeter in length in some cases. They may be scattered around the bundle, only above or below the bundle, arranged as a heavy layer above the bundle or as two small groups on either side of the resin canal. Variation seems to be caused by age of tree and position of the leaf on the tree.

Similar fibres of extreme length and closed lumen are often scattered between hypoderm and palisade on the upper side, or in addition to hypoderm between stomatal rows on lower side, but never form a distinct layer and are very rarely located at margins.

b. **AUXILIARY SCLERIDS:** In some species palisade cells are altered into pitted, thickened sclerids as shown in fig. 9. They are usually, but not always, much enlarged and the lumen remains large. Mesophyll cells are also sclerified in some species and are distinguished from the palisade sclerids by their position parallel to the cross section of the leaf blade and perpendicular to the palisade; and from the accessory transfusion tissue by their larger size and being shorter and wider. They may form a distinct layer between palisade and accessory transfusion tissue or they may be merely isolated.

Palisade: Except in cases where the palisade consists of two or three layers and shows this thickness consistently, this tissue cannot be used in identifying herbarium specimens. It is altered by light, moisture and age of leaf.

Stomata: Leaves are said to be hypostomatic when stomata are found only on one side (normally abaxially), amphistomatic when they are found on both sides. The latter may be further qualified when more stomata are to be found on one side than the other. Usually arranged longitudinally in rows, the number of rows is a function of the width of the leaf and varies accordingly. The rows may be crowded so as to be scarcely distinguishable, or they may be separated by several rows of ordinary epidermal cells. The subsidiary cell pattern of the stoma was considered in detail by Florin (5). Guard cells are flanked by two to four laterally adjacent and two polar cells and there may be a second rank or partial rank of such cells.

Cuticle: The thickness of the cuticle is an extremely variable character and there is not enough information concerning habitat available on herbarium specimens for correlation with cuticular thickness for this character to be useful except in very special cases.

In the cells of the first rank encircling the stoma, there may be a special furrow in the cuticular thickening forming a complete translucent ring. This was described by Florin (5) and we refer to this character as the Florin ring (compare figs. 11 and 12). Within section *Eupodocarpus* this

character is diagnostic in separating subsections A, C and D from subsection B. It may be present or absent in other sections where the character has been disregarded.

MATERIAL AND METHODS

The method for examination of cross sections of leaves of herbarium specimens of *Podocarpus* is quite simple. The leaf (more than one from different parts of twig or tree if abundant material is available) is soaked in distilled water until it sinks to the bottom of the vial. Then the leaf, or 1-2 cm. lengths from the midportion and base are placed in a split 3 cm.-length of elder pith. The sections are cut by hand with the *new* edge of a safety-razor blade and transferred to 50% glycerine. They may be examined in about an hour or, by evaporating out the water, permanent mounts may be made in glycerine jelly or the sections may be stored in vials in the pure glycerine. No staining of cross sections is necessary for any of the observations made in this paper.

To observe the epidermis, a 3-8 mm. section from the midportion of the leaf is macerated enough to separate the epidermis from the other tissues. The acid is washed out and it is then stained in a 50% solution of safranin. The stained epidermis is cleared and mounted in balsam. Thus the pattern of subsidiary cells of stomates and the Florin ring (fig. 11) as well as epidermal cell arrangement can be seen clearly.

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Dudley Herbarium (DS), United States National Herbarium (US), National Herbarium of Venezuela (Ven), Yale University Herbarium (YU), and Yale Forestry School (Y).

Podocarpus L'Heritier ex Persoon, Syn. 2: 580. 1807, *nomen conservandum*; Endlicher, Gen. Pl. 262, no. 1800. 1837, Syn. Conif. 206. 1847; L. C. & A. Richard, Comm. Bot. Conif. 124. 1826; Blume, Enum. Pl. Javae 1: 88. 1827; Bennett in Horsfield, Pl. Jav. Rar. 35. 1838; Carrière, Traité Conif. ed. 2, 643. 1867; Parlatores in DC. Prodr. 16(2): 507. 1868; Gordon, Pinetum ed. 2, 326. 1875; Bentham & Hooker f., Gen. Pl. 3: 434. 1880; Eichler in Nat. Pflanzenfam. II. 1: 104. 1889; Beissner, Handb. Nadelholz. 193. 1891; Pilger in Pflanzenreich IV. 5(Heft 18): 54. 1903, in Nat. Pflanzenfam. Nachtr. III, 4. 1906, and ed. 2, 13: 240. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 262. 1931, 19(2): 8. 1940, in Palaeontographica 85(B7): 577. 1944; Wasscher in Blumea 4: 360. 1941.

Nageia Gaertner, Fruct. Sem. 191. 1788, in part, description confused, *nomen rejiciendum*; O. Kuntze, Rev. Gen. 2: 789. 1891; Baillon, Hist. Pl. 12: 40. 1892.

Myrica sp. Thunb.; *Taxus* sp. Willd.; *Juniperus* sp. Roxb.

Coniferous trees or shrubs, usually dioecious, with large simple leaves, needle leaves or scale leaves, usually alternate (opposite decussate in section *Polypodiopsis*, sometimes subopposite in section *Nageia* and species of section *Afrocarpus*). Leaves amphistomatic or hypostomatic, with or without hypoderm, with transfusion tissue, with one resin canal always below the phloem of vascular bundle and sometimes additional resin canals between this and leaf margin, and as many as vascular bundles in section *Nageia*. Pollen cones cylindrical, terminal (section *Dacrycarpus*) or spicately arranged on lateral branches (section *Stachycarpus*) clustered on special peduncles or solitary, 1-3 fascicled in axils of leaves. Microsporangia 2 on each sporophyll, abaxial, dehiscing with a slit, usually with a centrally placed apiculus of sporophyll; pollen grains usually with 2 air-bladders or wings (or 3 or more in section *Dacrycarpus*). Ovulate cones terminal on short lateral twigs (sections *Microcarpus* and *Dacrycarpus*), or seldom spicate with separated ovules (section *Stachycarpus*), or with 1-2 ovules borne at or near the end of a special axillary fruiting branch, the strobilar axis beneath the seed remaining woody or becoming swollen fleshy at maturity. Ovules inverted, with micropyle near place of attachment, surrounded by and enclosed in an epimatium fused with seed coat except near micropyle and becoming coriaceous or fleshy with the middle layer of seed coat usually indurated, woody, or stony.

SUBDIVISION OF THE GENUS

The divisions of *Podocarpus* by Pilger in 1926 (13) following Engler (4) appears to us to be inconvenient and not well founded. His subgenera *Stachycarpus* and *Protopodocarpus* are each composed of heterogeneous assemblages of categories some of which appear to be more closely related to sections in the alternative subgenus than to each other. To set up additional subgenera in an effort to re-group them might cause more confusion than to list them all as sections. We agree with Wasscher (14) who states on page 361, "I doubt whether the subdivision into sub-genera is right. Perhaps we had better not distinguish any sub-genera, but only six equivalent groups which might be either sub-genera or sections." Our treatment is therefore in full agreement with Wasscher except that we are

adding two other sections for categories mostly outside of the range covered by his treatise. There is only one difference in sectional names: Wasscher's section *Stachycarpus* included plants which we are now placing in the new section *Sundacarpus*. Florin (5), p. 266, also suggested the advisability of such a revision.

The difference in our treatment of this genus and that of Pilger (13) may best be shown by the following outline:

Pilger (1926)	Present treatment
I. Subgen. <i>Stachycarpus</i> Engl.	
A and Ab	7. <i>Stachycarpus</i> Endl., in part.
B	{ 4. <i>Afrocarpus</i> n. sect. 6. <i>Sundacarpus</i> n. sect.
II. Subgen. <i>Protopodocarpus</i> Engl.	
Sect. 1. <i>Dacrycarpus</i> Endl.	1. <i>Dacrycarpus</i> Endl.
Sect. 2. <i>Microcarpus</i> Pilg.	2. <i>Microcarpus</i> Pilg.
Sect. 3. <i>Nageia</i> Endl.	3. <i>Nageia</i> Endl.
A. with swollen receptacle	A. with swollen receptacle
B. with woody receptacle	{ B. with woody receptacle 5. <i>Polypodiopsis</i> Bertrand
Sect. 4. <i>Eupodocarpus</i> Endl.	8. <i>Eupodocarpus</i> Endl.
A. without bracts beneath receptacle	{ A. African species. C. Central, S. American spp.
B. with bracts beneath receptacle	{ D. Chile, SW Pacific spp. B. Asia, S. Pacific, Austr.

KEY TO SECTIONS AND SUBSECTIONS

Leaves small, awl-shaped or scale like, amphistomatic, attached spirally.

Leaves of awl-shaped spreading needles, triangular or 4-sided in cross-section, with hypoderm, single resin canal; when flat, on pectinate frondose twigs of limited growth, giving the plants dimorphic foliage with the flat leaves compressed in vertical plane, ovule and seed with bract as long as ovule and fully incorporated with epimatium throughout its length; receptacle becoming swollen or fleshy as seed ripens (fig. 1).....Sect. 1. *Dacrycarpus*.

Leaves of loosely appressed scales, reddish, seed without fleshy receptacle and with bract shorter than seed, free from seed.....Sect. 2. *Microcarpus*.

Leaves large, not awl-shaped needles or scale leaves.

Leaves relatively broad with many parallel veins and as many resin canals beneath phloem, with hypoderm.....Sect. 3. *Nageia*.

Leaves amphistomatic, receptacle of seed becoming swollen and fleshy.....Subsect. A.

Leaves hypostomatic, receptacle of seed remaining woody.....Subsect. B.

Leaves with a single median vein.

Leaves amphistomatic, without accessory transfusion tissue.

Leaves alternate, spreading on all sides of twigs, seldom sub-opposite, with hypoderm on both sides, with transfusion tissue spread wing like from vascular bundle but without accessory transfusion tissue (fig. 3).....Sect. 4. *Afrocarpus*.

Leaves opposite, 4-ranked, decussate, but nevertheless usually spread out in a single plane (fig. 4).....Sect. 5. *Polypodiopsis*.

Leaves hypostomatic, or prevailingly hypostomatic.

Leaves without hypoderm.

Leaves large, not distichous, 5–16 cm. long (usually 8–11) and 6–14 mm. broad, with accessory transfusion tissue (fig. 2)..... Sect. 6. *Sundacarpus*.
 Leaves small, less than 3 cm. long and less than 5 mm. wide, usually spread apart in pectinate branches, (a few Old World species or their seedlings may be amphistomatic) without accessory transfusion tissue (fig. 7)..... Sect. 7. *Stachycarpus*.
 Leaves with hypoderm or hypodermal fibres, or if hypoderm is scanty, leaves with well developed accessory transfusion tissue, seeds with swollen, fleshy, or leathery receptacle..... Sect. 8. *Eupodocarpus*.
 Leaves with 3–5 resin canals, a pair of these near margin of leaf, bracts beneath receptacle absent, Florin ring present in subsidiary cells surrounding stomates (fig. 11)..... Subsect. A.
 Leaves with 1–3 resin canals, all at vascular bundle (figs. 5 & 8).
 Bracts present beneath receptacle, Florin ring absent (fig. 12).
 Subsect. B.
 Bracts absent beneath receptacle, Florin ring present (fig. 11).
 Accessory transfusion tissue well developed (fig. 9)..... Subsect. C.
 Accessory transfusion tissue absent or replaced by sclerids (fig. 10)..... Subsect. D.

Sect. 1. *Dacrycarpus* Endlicher, Syn. Conif. 221. 1847; Carrière, Traité Conif. ed. 2, 676. 1867; Parlatore in DC. Prodr. 16(2): 520. 1868; Pilger in Pflanzenreich IV. 5(Heft 18): 55. 1903, in Nat. Pflanzenfam. ed. 2, 13: 242, 245. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 267, 269. 1931, 19(2): 23, 69. 1940, in Palaeontographica 85(B7): 577. 1944; Wasscher in Blumea 4: 386–88. 1941.

Trees or shrubs with small alternate scale like, awl-shaped or flattened leaves, usually amphistomatic, with hypoderm, single resin canal beneath single midvein; dimorphic foliage may include distichous twigs of determinate growth with vertically flattened doubly falcate leaves appearing among branches with awl-shaped leaves, in these the vascular bundle may appear turned with xylem and resin canal on opposite sides of phloem. Pollen cones cylindrical, terminal on short lateral twigs with long apiculate sporophylls resembling leaves, with 2 sporangia; pollen with 3 or more wings. Ovulate cones terminal on lateral twigs with one or two inverted ovules (usually only one developing into seed) with bract adherent to and as long as ovule, becoming consolidated with epimatium throughout its length, the cone axis and sterile bracts below seeds usually becoming warty and fleshy. Southeastern Asia, East Indies and South Pacific Islands to New Zealand.

Sect. 2. *Microcarpus* Pilger in Pflanzenreich IV. 5(Heft 18): 58. 1903, in Nat. Pflanzenfam. ed. 2, 13: 243–245. 1926; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 270. 1931, in Palaeontographica 85(B7): 577. 1944.

Sect. *Dacrycarpus* Parlatore in DC. Prodr. 16(2): 520. 1868, in part; Vieillard ex Carrière, Traité Conif. 697. 1867.

Shrubs with small alternate scale like leaves, amphistomatic. Ovulate cones with small single crested ovule, with its bract free and much shorter than ovule or seed, with strobilar axis below seed not fleshy, but seed enclosed in epimatium surrounding stony seed coat. (*Podocarpus ussuriensis* Brongn. & Gris) New Caledonia.

Sect. 3. *Nageia* Endlicher, Syn. Conif. 207. 1847; Carrière, Traité Conif. ed. 2, 635. 1867; Parlatore in DC. Prodr. 16(2): 507. 1868; Pilger in Pflanzenreich IV. 5(Heft 18): 58. 1903, in Nat. Pflanzenfam. ed. 2, 13: 242, 245. 1926; Florin in

Svenska Vet.-Akad. Handl. ser. 3, 10(1): 272, 274. 1931, in *Palaeontographica* 85(B7): 578. 1944; Wasscher in *Blumea* 4: 415. 1944.

Trees and shrubs sometimes monoecious but mostly dioecious with leaves broad, having many parallel veins, either amphistomatic or hypostomatic, with resin canals beneath each of the many vascular bundles. Pollen cones cylindrical, single or several-fascicled at the end of an axillary peduncle. Ovulate cone at the terminal portion of an axillary fertile branch, a reduced strobilus whose scaly, many-noded axis may become fleshy or remain woody. Southeastern Asia, East Indies and Philippines to New Guinea.

Sect. 4. *Afrocarpus* sect. nov.

Sect. III *Stachycarpus* Endlicher, *Syn. Conif.* 218. 1847, in part; Pilger in *Pflanzenreich* IV. 5(Heft 18): 63. 1903, in part.

Subgen. *Stachycarpus* (Endl.) Engler in *Nat. Pflanzenfam. Nachtr.* 21. 1897; Pilger in *op. cit. ed. 2*, 13: 242. 1926, in part; Florin in *Svenska Vet.-Akad. Handl. ser. 3*, 10: 266. 1931, as "Artgruppe 2."

Arbores vel frutices dioici foliis magnis planis spiraliter dispositis, amphistomaticis, 1-vascularibus, ducto resinifero unico, fibrosis; strobilis masculis cylindricis, axillaribus, solitariis aggregatis; strobilis foemineis ramulo squamuoso proprio ligneo fultis; ovulis 1-2, anatropis, epimatio carnosus involucratis, a squamula saepius minore liberis; seminibus globulosis vel piriformibus; strato tegumenti medio indurato.

Africa from equatorial region southward. Type of section: *P. falcatus*.

Sect. 5. *Polypodiopsis* Bertrand in *Ann. Sci. Nat. ser. 5*, 20: 65. 1874; Florin in *Svenska Vet.-Akad. Handl. ser. 3*, 10(1): 275, 278, pl. 23, 30. 1931, 19(3): 8, 25, 71, pl. 1, 2. 1940, in *Palaeontographica* 85(B7): 578. 1944; Wasscher in *Blumea* 4: 423-427. 1941.

Sect. *Nageia* Pilger in *Pflanzenreich* IV. 5(Heft 18): 58. 1903, in part.

Subgenus *Protopodocarpus* Engler sect. *Nageia* Pilger in *Nat. Pflanzenfam. ed. 2*, 13: 245. 1926, in part, (B).

Dioecious trees with opposite (4-ranked decussate) foliage. Leaves small, amphistomatic, with single vascular bundle usually flanked by wing like appendages of transfusion tissue (as in *Afrocarpus*), with a resin canal beneath phloem and sometimes several to many other resin canals between center and leaf margin; hypoderm fibres present. Pollen cones cylindrical, 1 — several on the end of a special axillary branch with opposite pairs of scale leaves. Ovulate cone at end of an axillary fruiting branch, bearing terminally a single inverted ovule free from a small subtending bract, epimatium fused with and completely surrounding ovule and seed as part of a fleshy layer, sterile bracts of cone axis below seed scale-like decussate. Seed large, slightly elongated or pear-shaped. South America and South Pacific Islands, New Guinea, New Caledonia and Fiji.

Sect. 6. *Sundacarpus* sect. nov.

Podocarpus sect. 2 *Taxoideae*, Bennett in *Horsfield, Pl. Jav. Rar.* 40. 1838, in part. *Stachycarpus* Endlicher, *Syn. Conif.* 218. 1847, in part; Pilger in *Pflanzenreich* IV.

5(Heft 18): 63. 1903, in part.

Subgenus *Stachycarpus* Engler sect. *Nageia* Pilger in *Nat. Pflanzenfam. ed. 2*, 13: 245. 1926, in part, (B); Wasscher in *Blumea* 4: 380. 1944, in part.

Arbores dioicae foliis magnis planis spiraliter dispositis; foliis hypostomaticis, hypodermate parentibus, ducto resinifero saepius unico; strobilis masculis cylindricis, axillaribus, apice pedunculi brevis aggregatis; strobilis

foemineis pedunculo constantibus 1-3 ovulis bracteatis donato ad apicem inaequaliter dichotomo, squamulis ab ovulo liberis semper parvis; seminibus anatropis, epimatio carnosus, putamine duro.

East Indies, Philippine Islands, New Guinea, Cape York Peninsula of Australia. Type of section: *Podocarpus amarus* Blume.

Sect. 7. *Stachycarpus* Endl. (emend.), *Syn. Conif.* 218. 1847, in part; *Carrière, Traité Conif.* 672. 1867, in part; *Parlatore in DC. Prodr.* 16(2): 518. 1868, in part; *Eichler in Nat. Pflanzenfam. II, 1: 105.* 1889, in part; *Pilger in Pflanzenreich IV. 5(Heft 18): 63.* 1903, in part; *Florin, in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 266.* 1931, as "Artgruppe 1"; in *Palaeontographica* 85(B7): 577. 1944, in part.

Prumnopitys Phil. in *Linnaea* 30: 731. 1860.

Stachycarpus Van Tieghem in *Bull. Soc. Bot. France* 38: 162. 1891, as genus; *Engler in Nat. Pflanzenfam. ed. 1, Nachtr. 21,* 1897, as subgenus; *Pilger in op. cit. ed. 2, 13: 242.* 1926.

Dioecious trees with small spirally arranged leaves spread apart distically in one plane. Leaves of flattened needles usually hypostomatic, without hypoderm, with median vein, with transfusion tissue but without accessory transfusion tissue, a single resin canal beneath phloem. Pollen cones in spicate arrangement on special branches. Ovulate cones consisting of an axis bearing inverted bracted ovules in spicate arrangement on the end of a special fruiting branch of which several or only one may mature as a seed, or in some species only the terminal ovule may develop. Ovule and seed usually covered with soft epimatial layer which may form a distinct crest at the tip farthest from micropyle. Central and South America to New Zealand, Australia and New Caledonia.

Sect. 8. *Eupodocarpus* Endlicher, *Syn. Conif.* 208. 1847; *Bennett in Horsfield, Pl. Jav. Rar.* 39. 1838, as sect. 1; *Miquel, Fl. Ind. Bat.* 2: 1072. 1859; *Carrière, Traité Conif. ed. 2, 644.* 1867; *Parlatore in DC. Prodr.* 16(2): 509. 1868; *Gordon, Pinetum ed. 2; 326.* 1865; *Eichler in Nat. Pflanzenfam. II, 1: 104.* 1889; *Beissner, Handb. Nadelholz.* 193. 1891; *Pilger in Pflanzenreich IV. 5(Heft 18): 73.* 1903, in *Nat. Pflanzenfam. ed. 2, 13: 242, 247.* 1926; *Foxworthy in Philipp. Jour. Sci.* 6: 160. 1911; *Stiles in Ann. Bot.* 26: 448. 1912; *Gibbs in Ann. Bot.* 26: 543. 1912; *Hickel in Lecomte, Fl. Gén. Indo-Chine* 5: 1066. 1931; *Florin in Svenska Vet.-Akad. Handl. ser. 3, 10(1): 279, 283.* 1931, in *Palaeontographica* 85(B7): 577. 1944; *Wasscher in Blumea* 4: 427. 1941.

Trees and shrubs, usually dioecious, with alternate leaves arising from all sides of twigs. Leaves flat, hypostomatic, with hypoderm represented, with 1-5 resin canals, transfusion tissue, and accessory transfusion tissue with exceptions. Pollen cones axillary, single or grouped or variously clustered on peduncles. Ovulate cones borne singly on axillary peduncles bearing 1-2 terminal inverted ovules surrounded by epimatium, their subtending bracts separate and small, usually included in cone axis which, with sterile bracts, become a swollen or a fleshy receptacle. Seeds mostly ovoid or globose, frequently with an apiculus at exposed end, with the stony layer relatively thin. Central and South America, Africa, Asia, Australia, South Pacific Islands.

GEOGRAPHIC DISTRIBUTION

Three large areas of the tropics and southern hemisphere are occupied by species of *Podocarpus*. These are:

I. the area from southern Japan and China, Nepal, Sumatra to Australia including Tasmania and New Zealand, thence northward to the Fiji Islands and the Philippines.

II. South Africa and Madagascar extending northward only a few degrees north of the equator.

III. South and Central America northward almost to the Tropic of Cancer including the West Indies.

These three areas are geographically isolated by large oceanic expanses at the Equator and temperate zones and by the frigid zone in the Antarctic. The Indian Ocean and a gap formed by the peninsular part of India (where there are no conifers) separates I and II; the south Atlantic and Pacific Oceans isolate Area III.

In these three major areas the sections of *Podocarpus* are very unequally represented. Section *Eupodocarpus* is found in all of these areas, but the subsections differ. All other sections occupy either only one or parts of two of these larger areas.

Area I includes parts of seven of the eight sections of the genus which are unequally distributed and only two of the four subsections of *Eupodocarpus* which overlap. Within this region sect. *Microcarpus* is known only from New Caledonia, a relatively small island on which representatives of four other sections are encountered. Sections *Nageia* and subsection B of *Eupodocarpus* range farther northward in this area than species of *Podocarpus* anywhere else in the world, crossing the Tropic of Cancer and extending to about 34° N. latitude. The latter subsection covers almost the entire region of Area I excepting Tasmania and New Zealand. (Some of these plants may be cultivated in similar latitudes in the U. S. even though none of the native American species have spread north of the Tropic of Cancer on the American continent.)

In Area I the range of sect. *Sundacarpus* is restricted to the Sumatra-Philippine Islands-New Guinea triangle, overlapping and almost completely surrounded by the sections, *Nageia* and *Dacrycarpus*. The first two of these are not found east or far south of New Guinea, while section *Dacrycarpus* extends to New Zealand.

Australia has four sections represented, none of which is peculiar to this continent. All of them are extensions of the ranges of sections or subsections with extremely wide distributions. The range of section *Stachycarpus*, which touches northeastern Australia extends across the Pacific to South and Central America. Section *Eupodocarpus* is represented in Australia by two overlapping subsections, B and D. The former (B) ranges to China and Japan, and eastward to the Fiji Islands and New Caledonia, but not to New Zealand nor Tasmania, while the latter (D) ranges eastward across the Pacific from southeastern Australia, Tasmania, New Caledonia and New Zealand to Chile.

In Area II (Africa) only two sections are represented. Section *Afrocarpus* is found nowhere else, while subsection A of *Eupodocarpus*, with a similar distribution, includes Madagascar.

In Area III (America) three sections are represented: *Stachycarpus*, *Polypodiopsis* and subsections C and D of *Eupodocarpus*. All of these excepting C of *Eupodocarpus*, range across the south Pacific — *Polypodiopsis* from Venezuela and Peru to Fiji, New Caledonia and New Guinea; *Stachycarpus* from Venezuela and Costa Rica to New Zealand, New Caledonia and Queensland; subsection D from Chile to New Zealand, Tasmania, New South Wales and New Caledonia.

ORIGIN OF PODOCARPUS

The place of origin of *Podocarpus* would seem to be included in Area I where seven of the eight sections of the genus are represented. The tropics of Area I and well into the North Temperate Zone is a region inhabited by many species of Pinaceae, several Taxodiaceae, *Amentotaxus* and *Cephalotaxus*. Hence, if any single general area of the world may be designated, in which several or all of these families of conifers may have had a common origin, it is here where these diverse conifers still overlap. This is of special interest since their origin may go back to the close of the Paleozoic or not later than the early Mesozoic and it is known that there have been major changes in the continental areas since that time.

The conifers, with seeds as their only method of reproduction (before there were land animals other than amphibians and reptiles to aid in seed dispersal) probably spread very slowly. Their species never became truly world-wide. It may be presumed that some Podocarpaceae still occupy very largely the area or general region of their origin (sections *Nageia*, *Sundacarpus*, *Microcarpus*, *Dacrycarpus* and subsection B of *Eupodocarpus*). *Afrocarpus* and subsection A of *Eupodocarpus* may have migrated westward from Area I over land connections during an early period. Other sections such as *Stachycarpus*, *Polypodiopsis* and subsection D of *Eupodocarpus* have, on the contrary, spread themselves over areas incredibly distant, since they now occupy areas that are very far apart, with barriers of the South Pacific between.

The evolution of Podocarpaceae proceeded throughout the Mesozoic. They spread slowly until birds and mammals appeared, which might aid in the dissemination of their seeds. It must be remembered that conifers, cycads, ginkgos and ferns were the dominant land plants up until the sudden appearance of angiosperms in the Cretaceous.

However, Area II, with section *Afrocarpus* and subsection A of *Eupodocarpus*, is far removed from Area I. These areas must have been connected during the early Mesozoic and likewise Area III, which is separated from II by the Atlantic Ocean. Assuming no barriers, the mere spread of the plants of these sections to these areas must have required a long period of time.

There is evidence in leaf anatomy to indicate that sect. *Polypodiopsis* has characteristics in common with sect. *Afrocarpus* — amphistomatic leaves, well developed transfusion tissue into wing like expansions of the vascular bundle with the lack of accessory transfusion tissue (cf. figs. 3

& 4). There is also some evidence in leaf anatomy indicating that sub-section C and subsection A of *Eupodocarpus* have a common origin. This is indicated by the Florin ring (fig. 11) which they (along with D) have in common and by the absence of bracts beneath the receptacle (for these details see key to sections and subsections).

The apparent crossing of the South Pacific is also indicated by other genera in this family — *Dacrydium* with one species in Chile, *Araucaria* with two species in Area III and the remaining species in the southern part of Area I. Furthermore, sect. *Dacrycarpus* had a foothold in Chile during the Tertiary. Florin has demonstrated fossils in Chile that may be referred to this section. There are other conifers that appear to have crossed the South Pacific as well as primitive angiosperms.

These extreme migrations of several sections and their descendants which appear to have spanned several oceans in encircling the globe need not be believed if one accepts some form of the Wegener theory of continental drift. However, the sections of the genus must have been very unevenly distributed with their ranges widely diversified on Gondwana before separation of the continents took place. By using the maps given by DuToit (3, figs. 7 and 12, for example) one may account for the origin and dispersal of sections.

According to this, *Afrocarpus* and *Eupodocarpus* A (in Area II) would have come from or had an origin in common with *Podocarpus* of Area I. *Polypodiopsis* in Area III could have been derived from *Afrocarpus* in Area II and spread via Patagonia to New Caledonia and New Guinea. *Eupodocarpus* C could have come from *Eupodocarpus* A, giving rise, in turn, to *Eupodocarpus* D which reached New Zealand and Australia by the same route. The same holds for *Stachycarpus* except that we find some evidence in leaf anatomy to indicate migration in the opposite direction, from Australia and New Zealand via Patagonia to Central America. *Stachycarpus* may have been derived from *Sundacarpus* to which it is related and which has remained in Area I. The Wegener theory, therefore, serves to clear up many of the problems in the distribution of these and other conifers, to which there is no satisfactory alternative answer.

There is also the question as to which section of *Podocarpus* is most primitive. If the choice lies among the sections included in Area I, with seven sections represented, the selection is narrowed so very little that the decision must still be made on the basis of morphological characters. It is possible that some would contend the section *Eupodocarpus* to be one of the more primitive sections due to its wide distribution over all parts of the southern hemisphere. Our basis of judgment in placing this last is founded upon the almost universal hypostomate condition of the leaves and the well-developed accessory transfusion tissue (absent through loss in the course of evolution only in sub-section D). On the other hand, sections *Microcarpus* and *Dacrycarpus* include the small awl-shaped or scale leaves now known to be characteristic of primitive conifers (Florin 6). Section *Microcarpus* has the bract separated from the ovule which

would indicate that this section is more primitive than sect. *Dacrycarpus*. The latter may be advanced with respect to fusion of cone scale with the ovuliferous scale, represented by the epimatium, but is otherwise, in common with section *Microcarpus*, primitive in having the strobili borne on the ends of ordinary lateral branches rather than specialized fruiting branches. This is the condition shown by Florin (6) for several fossil conifers from the Paleozoic.

It was pointed out earlier by Buchholz (2) that embryologically section *Stachycarpus* in part (now section *Afrocarpus*) and *Nageia* may have the most primitive type of embryogeny. On this basis *Nageia* and *Afrocarpus* would seem to be among the more primitive sections. Furthermore the leaves of section *Nageia* have very much in common with another genus, *Agathis*, of which we have examined a number of species. *Agathis* differs primarily in having the resin canals situated between the vascular bundles rather than beneath them, next to the phloem. Indeed the leaves of sect. *Nageia* and *Agathis* also have much in common with those of certain fossil Cordaitales. Regardless of the precise point of origin in evolution, it appears unlikely from morphological considerations that *Polypodiopsis*, *Sundacarpus*, or *Eupodocarpus* are primitive.

Stachycarpus has been singled out by Wilde (15) as possessing a primitive type of grouping of strobili. This may be correct so far as it concerns the arrangement of pollen cones and seed cones, but not necessarily the origin of the strobilar structure itself. There is still a gap between the specialized branch, bearing cones, and the cone borne terminally at the end of a lateral unspecialized branch. There is the question, therefore, whether the condition of *Dacrycarpus* stands at the end of a reduction series from a specialized branch bearing clustered cones, or whether this solitary terminal cone on an unspecialized branch may not represent a more primitive condition, before specialized branches arose. Wilde treats sect. *Dacrycarpus* as if it were derived from sect. *Stachycarpus*. As we have observed in numerous specimens belonging to sect. *Dacrycarpus*, we are inclined to agree with Wasscher's description of these cones, namely, that they are terminal on short lateral unspecialized twigs in which the leaves of these twigs gradually merge into the little-different microsporophylls.

It may be pointed out that Wilde's (15) arrangement of female cones in the entire series for the genus is realized fully within the sect. *Stachycarpus*, even as we have restricted this category. Here, as she points out, *Podocarpus andinus* and *P. spicatus* show the most primitive condition among living forms, whereas, *P. montanus*, in which only a single ovule (sometimes two) remains to form the seed in a terminal position, represents an end member as extreme as any of the others which she cites. In *P. montanus*, of which we are including views of the female fertile branches (figs. 19, 24, 27), not only is the foliage that clothes this member composed entirely of normal leaves, but even the bract subtending the terminal ovule has become enlarged and leaf-like.

Among the sections, our choice of the most primitive has narrowed down to one of three: *Microcarpus*, *Dacrycarpus* and *Nageia*. All of the others save *Afrocarpus* may be excluded. These three sections are the ones about which least is known morphologically — not even the taxonomic characters are fully understood.

Our order of numbering the sections therefore has little significance. Among the three most primitive we are retaining the order given by Pilger in 1903 (12), very largely as a matter of convenience.

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A TAXONOMIC REVISION OF PODOCARPUS

II. THE AMERICAN SPECIES OF PODOCARPUS: SECTION STACHYCARPUS

JOHN T. BUCHHOLZ AND NETTA E. GRAY

With four plates

SPECIES of *Podocarpus* belonging to section *Stachycarpus* have small yew-like leaves, spread apart distichously, are without hypoderm, with transfusion tissue, and have no accessory transfusion tissue. They may be distinguished from those of *Taxus* by the presence of the single resin canal, absent in *Taxus*. All American species are hypostomatic, but there are several species in the Old World near the extreme western limit of the range of this section with unequally amphistomatic leaves. (In this region there might be confusion with certain species of *Dacrydium* which are usually not distichous though some are without hypoderm.)

In differentiating the species in this section it has been found that the plants are so similar in leaf anatomy that it is impossible to distinguish the American species from each other through internal differences. The greatest variation is observed in the number of layers of palisade tissue but this character is somewhat subject to ecological conditions such as altitude and exposure. There is no sclerenchymatous tissue, nor isolated sclerids whatever, aside from that belonging to the vascular bundle and its associated transfusion tissue. Externally, some usable differences are readily visible — groove vs. ridge or flat surface above the midvein, size and shape of leaves. But to make positive identification, seed cones and seeds are necessary. Unfortunately, not many of the specimens collected are with seeds. It is therefore possible that some of the varieties may represent distinct species but a great deal of field observation by botanical collectors and foresters is necessary to delimit the natural ranges of the species and varieties, and to amplify the descriptions of the mature trees as well as the reproductive parts.

KEY TO THE NEW WORLD SPECIES OF PODOCARPUS BELONGING TO SECTIONS STACHYCARPUS AND POLYPODIOPSIS

Leaves flat, attached spirally, distichous, linear or oblong-linear, sometimes falcate; with a single midvein and resin canal, without a layer of hypodermal cells, with well developed palisade tissue and with stomates confined to lower (abaxial) surface.....Section *Stachycarpus*.
Leaves flat above or with a slight ridge above the midvein (figs. 13-17, 21, 22).
Leaves nearly flat above, 15-24 mm. long, about 1.5 mm. wide; seeds ovoid, 20 mm. long, 13-14 mm. wide, very little flattened, borne singly or with several on a spike which is a strobilar axis bearing numerous ovules at the time of pollination. South of Equator.....1. *P. andinus*.

Leaves with a slight ridge above the midvein.

Leaves usually 15–24 mm. long, up to 3.5–4.5 mm. wide, falcate; seeds 9–10 mm. long, with a fleshy coat drying as in a plum, the ovules numerous and borne on an axis resembling a spike, as in *P. andinus* (figs. 13, 17, 21–23). North of Equator.....2. *P. Harmsianus*.

Leaves less than 18 mm. long, seldom more than 2 mm. wide; seeds unknown, ovules borne as in *P. andinus* (figs. 14–16), single crested. South of Equator.....3. *P. utilior*.

Leaves with groove above midvein (fig. 20). North of Equator.

Female reproductive branch bearing ordinary leaves fully or nearly same size as foliage leaves; leaves 5–20 mm. long, 2–4 mm. wide, acute or obtuse.

Leaves 12–20 mm. long, 2.5–4 mm. wide, mostly acute; dry seed up to 15 mm. long, 8–10 mm. wide, with single flattened crest 3–4 mm. long (figs. 24 & 25).....4. *P. montanus*.

Leaves 5–12 mm. long, 2–3 mm. wide, mostly obtuse; seed about 12 mm. long, 8–9 mm. wide, bearing 2 distinct, bluntly rounded crests (figs. 27 & 28).....5. *P. montanus* var. *densifolius*.

Leaves 7–14 mm. long, 2.5–3.5 mm. wide, mostly obtuse (groove sometimes broad and open); dry seed about 10–13 mm. long, 6–8 mm. wide, crest of fused spines or appearing single, relatively long and slender (figs. 19, 29–31).....6. *P. montanus* var. *meridensis*.

Female reproductive branch bearing small bracts or scales, leaves 15–25 mm. long, 2.5–3.5 mm. wide; seed 10–11 mm. long with cylindrical crest 2 mm. long (figs. 32–34).....7. *P. Standleyi*.

Leaves ovate, sessile, opposite, 4-ranked but spread out in a single plane; with stomates on both sides, with hypoderm, a single midvein and 3–11 resin canals.Section *Polypodiopsis*.

8. *P. Rospigliosii*.

1. *Podocarpus andinus* Poeppig ex Endlicher Syn. Conif. 219. 1847; Gay in Flora Chilena 5: 403. "1849" [1852]; Gordon, Pinetum 351. 1875; Pilger in Pflanzenreich IV. 5(Heft 18): 64. 1903; Reiche in Engler & Drude, Veg. der Erde 8: 63–64. 1907; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 262. 1931; Covas in Rev. Argent. Agron. 6: 24. 1939.

Podocarpus spicata sensu Poeppig, Nov. Gen. Sp. 3: 18. 1845, non R. Br.

Podocarpus valdiviana Senilis, Pinaceae 160. 1866.

Prumnopitys elegans Phil. in Linnaea 30: 731. 1860; Carrière, Traité Conif. 682. 1867; Dallimore & Jackson, Handb. Conif. 60. 1923, 1931.

Stachycarpus andina Van Tiegh. in Bull. Soc. Bot. France 38: 173. 1891.

Taxus spicata Dombey ex Gordon, Pinetum 351. 1875.

An evergreen pyramidal tree becoming 12 m. high, though often only a shrub in cultivation, with smooth dark reddish brown bark, extensively branched and with numerous branchlets. Twigs short, subalternate with many leaves, spreading pectinately. Leaves linear, thin leathery, bright green above and glaucous beneath, straight or only slightly falcate, short-mucronate, or often obtuse at the tip, somewhat narrowed at the base which is fairly broad, with midvein inconspicuous on upper side, much more prominent beneath especially toward the base, 15–24 mm. long and usually 1.5 or less than 2 mm. wide. Pollen cones borne spicately on a special lateral branch 1.5–2.5 cm. long, among leafy twigs; cones divariccate, numerous (12–20), 6–8 mm. long, sessile, in the axils of minute bracts and crowded toward tip of the branch. Microsporophylls with 2 pollen sacs, terminated by a broadly triangular upturned flat tip, with scarious and minutely denticular margin. Seed cone, a greatly modified strobilar axis appearing as a spike on the end of a special branch 2–2.5

cm. long, with leaves below, followed by scales and bearing several (3–5 or more) scattered ovules above in the axils of small bracts with only one or two of them maturing as seeds attached laterally to the strobilar axis. Seeds ovoid, with a stony inner and a fleshy outer layer resembling a drupe, 20 mm. long, 13–14 mm. wide, slightly flattened. Outer fleshy layer dries over the stony layer as in a miniature prune.

DISTRIBUTION: Central to south-central Chile.

SPECIMENS EXAMINED:

CHILE. Valdivia: Cordillera de la Costa, Poeppig (†A, US); Union, at banks of stream near Ranco, Anon. (US, with pollen cones). Chile, without detailed locality: "Austro-Andina," Feb. 1829, Poeppig, ISOTYPE (ex Bernhardi Herb.) (†Mo, †F); Ruiz 4635 (ex Herb. Lambert; US); Germain (†GH, with seeds); Philippi, in 1888 (†A, with seeds, NY [fig. 26], US). CULTIVATED: Kew, Nicholson, in 1884 (A); R. N. Parker, in 1903 (A); Hanover, Muenden, H. Zabel (A); Mainau Island, Lake Constance, Schneider, Sept. 1903 (A); Silesia, Breslau, Baenitz, 1170 (US, GH); "Greendale," Anon. (A, with excellent pollen cones); Golden Gate Park, San Francisco, Walther, in 1931 (CAS); Buchholz in 1942 (III.).

Podocarpus andinus was described by Endlicher who attributed the name and description to Poeppig, indicating an earlier report of this entity under the name of *P. spicatus*, a New Zealand species. Later Philippi described the same plant under a separate generic name as *Prumnopitys elegans*. This is clearly a superfluous name, and therefore, illegitimate, but somehow it has persisted as a horticultural trade name and is still in use. Dallimore & Jackson (1923, 1931) place all species of this group under *Podocarpus* except this one, which they describe under a separate genus as *Prumnopitys elegans* Philippi.

2. *Podocarpus Harmsianus* Pilger in Pflanzenreich IV. 5 (Heft 18): 68. 1903; Dallimore & Jackson, Handb. Conif. 47. 1923, 1931; Pittier, in Bol. Cient. y Tecn. Mus. Com. 1: 9. 1927; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 262. 1931; Macbride, Flora of Peru, 1 (Field Mus. Nat. Hist. Publ. 351, Bot. ser. 13): 83. 1936; Schnee in Bol. Soc. Venezol. Cienc. Nat. 9: 184–5 (excl. fig. 3 = *P. montanus meridensis*), in part. 1944.

An evergreen tree with dark brown scaly bark becoming 15 m. high or higher with a trunk diameter up to 40 cm. Branchlets slender and somewhat loosely leaved. Leaves coriaceous, spirally arranged, distichously spread in one plane, patent, oblong-lanceolate, straight or falcate or somewhat s-shaped, acute or short angustate above and below, narrowly sessile, 15–27 mm. long, 3–5 mm. wide, pruinose when young except at midrib which is obtusely prominent above and less prominent or flat beneath where midvein separates the two bands of stomates. Pollen cones divaricate, about 15 in each spike, up to 10 mm. long and borne in the axils of minute elliptical, acute bracts (these 2 mm. long), surrounded at the base by small imbricated scales. Microsporophylls broad with a large triangular obtuse upturned apex lacerated at the margins, with two laterally placed microsporangia dehiscing laterally and horizontally. Ovulate cones greatly reduced, consisting of a slender modified branch 15–25 mm. long, clothed only with minute scales below (soon deciduous). Strobilar axis

† This symbol preceding the abbreviated name of an herbarium following the specimens examined signifies that the details of the leaves of this specimen have been examined in cross-section.

bearing one or more inverted ovules near tip, attached laterally in the axil of a bract half as long as the ovule. Seed not flattened, only slightly crested and with a thin fleshy outer seed coat not greatly wrinkled in drying.

SPECIMENS EXAMINED:

VENEZUELA: *Colonia Tovar* (= Tovar in Aragua): *Fendler 1289* Berlin ex Pilger LECTOTYPE; *Fendler 1289*, ISOTYPES (GH with pollen cones, Ph [fig. 13], †Mo); *Delgado 174* TOPOTYPE (†F with seed of *P. Rospigliosii* (?) in pocket, US without seed); *Delgado 206* (†US); Alto de Nor Leon, *Alfredo Jahn* TOPOTYPE with ovulate strobilus [fig. 21] (†US). Distr. Federal: Silla de Caracas, *O. Kuntze 1611* (NY, US, †F); *Steyermark 55146* (F, III); *Delgado 338* (Ven).

COLUMBIA: Magdalena: San Lorenzo Mts. near Santa Marta, *Viereck*, Dec. 1922, (†US with seeds and female strobilus in pocket, [figs. 17 & 23] (F). Colombia, without locality: *Karsten 287* (photo.) probably belongs here (F).

CULTIVATED: Guatemala, garden of Don Mariano Pancheco H., *Steyermark 39887* (†F); Venezuela, *Colonia Tovar, Tamayo 1575* [fig. 22] (†Ven); Colombia, Minca, *Bro. Apolinar A625* (†US); *Daniel 3349* (†US).

The differences between the Colombian and Venezuelan specimens of *Podocarpus Harmsianus* seem to be only slight. More intensive study may reveal differences sufficient to warrant a variety. If so, the Venezuelan plants should be considered as representing the typical form of the species.

Pilger cited two specimens under the original description of this species, listed alphabetically — Colombia without locality *Karsten 287* and Venezuela, *Colonia Tovar* (= Tovar in Aragua), *Fendler 1289*. The first specimen cited has been selected as the type by Macbride for the collection of photographs. This arbitrary choice by Macbride is unfortunate, since the Karsten specimen is sterile, without locality and has now been destroyed with the Berlin collections.

A study of Pilger's description reveals that the whole of the text applies to the Venezuelan plant, for this is the only one that included pollen cones. The Karsten photograph shows longer leaves, suggesting a seedling or juvenile specimen. Only about half of the description could apply to this sheet. Duplicates of the Fendler specimen are found in American herbaria and one of these (GH) includes the reproductive parts. We, therefore, designate *Fendler 1289* as the lectotype of this species.

3. *Podocarpus utilior* Pilger in Fedde, Rep. Nov. Spec. 1: 189. 1905; Weberbauer in Veg. der Erde 12: 74. 1911; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 262. 1931; Macbride, Flora of Peru, 1 (Field Mus. Nat. Hist. Publ. 351, Bot. Ser. 13): 84. 1936.

Podocarpus montanus sensu Britton in. Bull. Torrey Bot. Club 16: 13. 1889, not (Willd.) Lodd.

An evergreen tree up to 20 m. or more high with many branches, the branchlets spreading or erect to spreading, very leafy. Leaves borne spirally but spreading out distichously in one plane, crowded, patent, small, thick, linear, coriaceous, often somewhat widest above the middle, acute or obtuse, oblique at base, sessile or very short-petioled, 10–18 mm. long, about 1.5–2.5 mm. broad, midrib slightly prominent above, with streaks beneath, except along the midrib, but not glaucous. Leaves of seedlings and young trees probably larger. Pollen cones unknown. Seed cones reduced to a special branch 15–30 mm. long surrounded at the base

by a few deciduous scales and ending in a strobilar axis bearing 4-6 bracted inverted ovules in spiral arrangement, the ovules prominently crested with a single spine-like point. Seeds unknown.

SPECIMENS EXAMINED:

PERU: Junin: Tarma, Mt. Yananga, east of Haucapitana, photo. of type and fragment *Weberbauer* 2114 (\dagger F Neg. no. 11580, fragment from Florin ex Berlin Herb. \dagger , [figs. 14, 15]); Oxapampa, *Soukup* 1802 (GH, \dagger US, \dagger Ill with female strobili [fig. 16]). The following sterile specimens may be referred to *P. utilior* mostly on the basis of geography and agreement in leaf structure even though larger: Ayacucho: Ocarapapa, *Killip and Smith* 22480 (\dagger A, \dagger F, NY, US); Junin, Pichis Trail, *Killip and Smith* 25746 (\dagger US seedling).

BOLIVIA: Yungas, *Rusby* 1960 (\dagger NY, Mich); Huainachoirisa, *Williams* 1535 (\dagger NY); Santa Cruz: Samaipata, *Carriker* (\dagger Ph, this specimen has no ridge above midvein, is actually somewhat concave-depressed above).

CULTIVATED: Berlin Bot. Gard., *Rehder* in 1885 (A); ex Gord. Herb. (A); Naples, Hort. Bot. Neapol., *Engelmann* in 1868 (Mo).

As the name implies, this tree is locally used as a source of lumber. Figure 20, supplied by Mr. J. Soukup, shows recent logging operations at Oxapampa. These large logs 1.75 m. in diameter are presumably of this species but this is not a certainty since *P. Rospigliosii* is known to occur also in this locality. The latter is a much smaller tree.

While mature seeds have not been available, fig. 15 of the type specimen of *P. utilior* shows some of the ovules beginning to enlarge, bearing single long spine-like crests. Partially enlarged ovules of *P. Harmsianus* have not shown traces of the crested condition. Its mature seeds are crestless or show a very blunt crest; also this tree is not known to approach the size of *P. utilior* shown in fig. 20. The seeds of *P. Harmsianus* which mature are usually subterminal, those of *P. utilior* show several lateral ovules developing.

The leaves of these two species are very similar. Those of *P. utilior* are smaller in general and are much smaller in the type specimen than those of *P. Harmsianus*. Presumably, reproductive branches taken far up near the top of a large tree would have smaller leaves. The collections of *Soukup* 1802 are reproductive in the U. of Ill. specimen (fig. 16) and have leaves larger than the type. Presumably the size of the leaf of *P. utilior* varies greatly depending upon the position on the tree and upon the size of the plant, so that shrubby specimens may have much larger leaves than mature trees. In this condition they may be indistinguishable from those of *P. Harmsianus*, but the latter have not been found to be as small as the type of *P. utilior*, on any specimens. Small seedlings of both of the species have been seen, and have long, relatively slender leaves.

On the assumption that only a single species has been found in Peru, we are including the material of seedlings and shrubby plants collected by Killip & Smith with rather large leaves under *P. utilior*. This decision is also supported on the basis of geography. With no collections before us from central and southern Colombia or Ecuador with a ridge above the midvein of the leaves, we feel convinced that this geographic discontinuity indicates two distinct but closely related species.

Prior to Pilger's monograph (1903) only a single species in this group was recognized. All specimens are referred to *P. taxifolius* = *P. montanus*. No distinction has been made with respect to a groove vs. ridge above the midvein. However, the plant now known as *P. utilior* was found in cultivation in European gardens—this or *P. Harmsianus*. Gordon in the Pinetum (1858 and 1875) describes the species as known to him "with a slight rib along the upper surface." Witness also the cultivated specimens cited above: Rehder in 1885 from the Berlin Botanical Gardens and a specimen from the Gordon Herbarium. Both of these have the ridge.

All early references give Peru as the origin of *P. montanus*. The original type specimen of *Taxus montanus* Willd. has a distinct groove above the midvein, clearly shown in the photograph. These earliest collections actually came from near Loja in Ecuador and from Colombia, not Peru. No Peruvian specimen of *P. montanus* has been found among those available in American collections. However, all plants that agreed with the early descriptions, grown from seeds of Peruvian origin passed under the name of the only described species and it may be inferred that the plant now known as *P. utilior* was actually in cultivation in Europe for more than a half century before *P. utilior* was described.

Macbride included *P. montanus* in his Flora of Peru based upon material collected by Humboldt on Mt. Saraguro across the border in Ecuador. It might, therefore, be encountered in northern Peru but has not been collected there thus far.

4. *Podocarpus montanus* (Willd.) Loddiges, Cat. 37. 1836; Pilger in Pflanzenreich IV. 5 (Heft 18): 67. 1903, *in part*, in Nat. Pflanzenfam., ed. 2, 13: 245. 1926, in part; Dallimore & Jackson, Handb. Conif. 51. 1923, 1931, in part; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 262. 1931; Macbride; Flora of Peru, 1 (Field Mus. Nat. Hist. Publ. 351, Bot. Ser. 13): 83. 1936.

Podocarpus montanus var. *diversifolius* Dallimore & Jackson, Handb. Conif. 51. 1923, 1931.

Podocarpus Harmsianus sensu Schnee in Bol. Soc. Venezol. Cienc. Nat. 9: 184-6. 1944, not Pilg.

Dacrydium distichum Don ex Lamb. Pinus, ed. 2, 2: 120. 1828.

Nageia montana O. Kuntze, Rev. Gen. 2: 800. 1891.

Podocarpus taxifolia Kunth, in Humb. and Bonpl., Nov. Gen. 2: 2, pl. 97. 1817; L.C. & A. Richard, Comm. Bot. Conif. 15. 1826; Endlicher, Syn. Conif. 219. 1847; Gordon, Pinetum 288. 1858, 355. 1875, in part; Carrière, Traité Conif. ed. 2, 672. 1867; Parlato in DC. Prodr. 16(2): 518. 1868; Uribe, Flora de Antioquia Medellin 44. 1940.

Podocarpus Humboldtii Hort. ex Gordon, Pinetum 288. 1858, 355. 1875.

Prumnopitys taxifolia Hort. ex Dallimore & Jackson, Handb. Conif. 51. 1923, 1931.

Stachycarpus taxifolia Van Tiegh. in Bull. Soc. Bot. France 28: 173. 1891.

Taxus montana Willd. Spec. Plant. 4(2): 857. 1805, not Nuttall.

Torreya Humboldti Hort. ex Lindl. & Gord. in Jour. Hort. Soc. 5: 355. 1850; Knight ex Gord. Pinetum 355. 1875.

An evergreen tree up to 25 m. tall with wide-spreading branches bearing numerous alternate branchlets with taxoid foliage. Leaves spirally arranged and spread out distichously in one plane, linear, sometimes oblique or falcate, apex acute, broadly acute or mucronately acute, gradually narrowed at the subsessile base, sub-petioled, 10-18 mm. long, 2.5-3.5 mm.

wide, dark green above, paler beneath, with a distinct groove above the midvein which is slightly prominent beneath between two broad bands of stomates. Pollen cones numerous (up to 25) spicately arranged on the end of a special branch 3-5 cm. long, each cone borne in the axil of a small ovate bract (this 2-3 mm. long). The cones patent about 10 mm. long, sessile toward the end of the special branch but with peduncles up to 3 mm. long in the lowest cones. Microsporophylls broad with a pair of ovoid sporangia dehiscing horizontally, the upturned apex of the sporophylls triangular from a broad base, obtusely rounded with a scarious margin. Pollen 2-winged. Seed cone reduced to the end of a small branch 4-6 cm. long bearing ordinary leaves below, and only a few bracted inverted ovules at its tip, only the terminal ovule developing into a fleshy seed, the strobilar axis not becoming fleshy. Seed ovoid-globose, sessile, 14 mm. long, 8-9 mm. thick, tipped with a single, somewhat flattened crest, the fleshy outer layer wrinkled upon drying.

Type specimen not seen. Plate 97, vol. 2, Humboldt & Bonpland (1817) shows presumed type specimen; locality, according to Kunth: Quindiu Pass (in Colombia near $4^{\circ} 38'$ N. Lat.; $75^{\circ} 42'$ W. Long.)

DISTRIBUTION: central cordillera in Colombia and Ecuador.

SPECIMENS EXAMINED:

COLOMBIA: Cauca, western slopes of Paramo de Moras, Lehmann 3763 (\dagger US); Musillo, Central Cordillera, Dawe 747 (NY, US); Caldas, San Felix near Salamma, Bro. Thomas 2050 (US); Colombia (New Granada) without specific locality: Rev. Holton in 1854 ex Torrey Herb. [fig. 18] (\dagger NY); Triana 511 (\dagger US); Mutis 641, 3858, 4414 (US); Bro. Ariste Joseph A897 (\dagger US).

ECUADOR: Loja, between Tambo Cachiyacu and Nudo de Sabinillas, Steyermark 54472 (F with seeds, [figs. 24 & 25], III).

It should be noted that we have included Dawe 747 bearing the annotation that this is an important timber tree of the central cordillera in Colombia as representative of the species. Dallimore & Jackson mention this Dawe collection under a trinomial *P. montanus diversifolius* (they may have intended *densifolius* Kunth) which has leaves that are shorter than those of Costa Rican collections, but somewhat longer than those of the variety *densifolius* (see below). Unfortunately no seeds are included among the Dawe specimens, which therefore lack the completeness necessary for more definite classification.

The combination *P. montanus* var. *diversifolius* Dallimore & Jackson is a superfluous name, in any case illegitimate whether it belongs under the variety *densifolius* Kunth or under the species.

5. *Podocarpus montanus* var. *densifolius* (Kunth) comb. nov.

Taxus montanus var. (without name) Willd. Sp. Pl. 4(2): 857. 1805.

Podocarpus taxifolia var. β : *densifolia* Kunth in Humb. and Bonpl. Nov. Gen. 2: 2. 1817.

Podocarpus taxifolia densifolia (Kunth) Gordon, Pinetum 289, 1858. 355, 1875; Carrière, Traité Conif. ed. 2, 673, 1867.

An evergreen tree differing from the above species in its more crowded, shorter, more obtuse leaves, 6-12 mm. long, 2-3.5 mm. wide, dark green above, paler but not glaucous beneath; ovules borne as in the above species but double crested. Seeds about 14 mm. long, 8-9 mm. wide, with a pair of blunt crests.

Type specimen not seen; presumed to be *Link* in Berlin Herb., Photograph in Collection of American types in European Herbaria, Neg. #11575, (F).

Type locality: a few authors including Gordon cite Humboldt in giving the Mountains of Saraguro between Ona and Loja by error in Peru; actually this is in Ecuador. Both the species and the variety appear to be found here and in Colombia and have been collected since in the two regions.

SPECIMENS EXAMINED:

COLOMBIA: Bogota, *Purdie*, sent to Hooker about 1849 (ex Bentham Herb.) with ♀ strobilus, seed in packet (†NY [fig. 27]); *Purdie*, sent to Torrey and Gray, no date (NY, G); Cundinamarca, Sibate, shrub or young tree, *Pennell* 2436 (Ph, GH, †NY, [fig. 28] US, F).

ECUADOR: Azuay, beyond Sayousi on trail to Cajas, *Penland & Summers* 1082 (F).

6. *Podocarpus montanus* var. *meridensis* var. nov.

Podocarpus montanus Pilger, *Pflanzenreich* IV. 5 (Heft 18): 67. 1903, in part, in *Nat. Pflanzenfam.* ed. 2, 13: 245. 1926, in part.

Podocarpus Harmsianus Schnee in *Bol. Soc. Venezol. Cienc. Nat.* 9: 184-5. 1944, not Pilger.

Podocarpus montanus Schnee, *ibid.* in part.

Semine quam in *P. montano* ejusque var. *densifolio* minore differt; seminis crista saepius processibus spinosis geminis confluentibus efformata, vel processibus totis coalescentibus semen *P. montani* valde diminutum mentiente; foliis *P. montani* var. *densifoli* persimilibus vel statura intermedia, canaliculo per costam interdum magis aperto.

SPECIMENS EXAMINED:

VENEZUELA: Lara, between Buenos Aires and Páramo de las Rosas, *Steyermark* 55459 (F, Ill); Trujillo, Cerra de La Mesa de Esmujaque, *Schnee* 50 (Ven, †Ill); *Schnee* 55 (Ven, †Ill); Merida, Timotes, *Delgado* 366 (†Ven [fig. 29]); Arriba de Chachopo, *Schnee* 33 (Ven, †Ill); Tachira, below Páramo de la Negra, above La Grita, *Steyermark* 57103 (F, Ill TYPE [fig. 19]); *Klugh* in 1944 (†Ven [fig. 30]).

COLOMBIA: Magdalena, Cerro Pintado, Sierra Perija, *Carricker* 49 (US).

This variety of *P. montanus* with leaves that are very similar to or intermediate between the species and var. *densifolius* in size, appears to be widely distributed and somewhat more frequently encountered than the others, with an eastward extension to Lara in Venezuela. However, the seed is not intermediate in size, but is smaller, and furnishes a more distinctive characteristic in its crest. The crest is composed of a pair of partially fused spine-like projections, or these spines may be completely fused resembling the seeds of *P. montanus*, but the entire seed is much smaller. Schnee (1944) was led astray by these spines, regarding them as characteristic of the seeds of *P. Harmsianus* Pilg. of which seeds had not been seen thus far; where actually collected, the specimens had been referred to *P. montanus* by some Venezuelan botanists. As shown in our key, *P. Harmsianus* and *P. utilior* have a ridge on the upper side of the leaf, while the members of the *montanus* group have a distinct groove over the midvein. However, this groove may be somewhat open (fig. 7) in the specimens of var. *meridensis*.

It is possible that both the varieties under *P. montanus* should be regarded as distinct species. There is considerable variation among specimens both as to the leaf and seed characters. We feel that careful observation of these characters by foresters and collectors is desirable before establishing these entities as distinct species, and that our treatment of the specimens before us will serve adequately to bring them to the attention of collectors.

7. *Podocarpus Standleyi* nov. sp.*

Podocarpus montanus sensu Pilger in *Pflanzenreich* IV. 5 (Heft 18): 67. 1903; in *Nat. Pflanzenfam.* ed. 2, 13: 245. 1926, in part; sensu Standley, *Flora Costa Rica*, *Field Mus. Nat. Hist. Publ.* 391, *Bot. ser.* 18: 64. 1937.

Arbor sempervirens 25 m. alta, ramulis foliosis alternatum patentibus numerosis; foliis linearibus spiraliter dispositis, uno plano patentibus, saepius falcatis, deorsum acutis vel mucronatio-acutis, ad basim gradatim angustatis, late breviterque subpetiolatis, 12–25 mm. longis (pro more 14–18), 2.5–3.5 mm. latis, supra ad costam, manifeste canaliculatis, costa subtus prominente utrinque zona stomatifera notata; foliis hypostomaticis, regione chlorenchymatis subinde cum epidermate finitima (i.e., strato hypodermico nullo), ducto resinifero sub vena unico; strobilis ♂ in ramulo proprio spicatum dispositis, numerosis (ad 20), apicalibus sessilibus, infernis subsessilibus, in anthesi (i.e., pollinis effusi tempore) ca. 10 mm. longis, bracteis minutis ovatis fultis; microsporophyllis latis, sporangiis 2 ovoideis, basi latis, in apicem triangularem excurvatis, margine libero laevi, scarioso, denticulato; microsporangii transversim dehiscentibus, polline alato; strobilis ♀ in apice ramuli spiralis 15–25 mm. longis fultis, foliis minimis vel squamis praeditis quam foliis eufoliaceis multo minoribus; ovulis inter sessilibus paucis bracteatis, ad apicem ramuli proprii insidentibus in axin strobili confluenti, terminali semen unicum praebenti maturum; seminibus globoso-ovoideis, crista gracili cylindrico-conica 2 mm. longa coronatis, semine toto 10.5 mm. longo, ca. 6 mm. lato, haud complanato, sicco extus tantum minute ruguloso.

SPECIMENS EXAMINED:

COSTA RICA: Volcan de Poas: Mts. of Canton de Dota, *Tonduz* 10333, TYPE, immature ♂, ♀ cones with seed [fig. 33] in packet (†US); *Tonduz* 10743, ♀ cone [fig. 32] (US); *J. D. Smith* 6857 (†GH, US [fig. 34]); *Standley* 34836 (US); *Haupt* in 1940 (†LA); *Roever* 5074 (NJU); La Laguna, *Tonduz* 11913 (US); *Standley* 42347 (†F, US); San José, Cerro de las Vueltas, *Standley & Valerio* 43581 (†F, US); Cartago, Camp Empalme, along Pan American Hy., *Little* 6030 (F).

In describing *P. Standleyi* we are restricting Pilger's description of *P. montanus*. Pilger had broadened the description in including Costa Rican plants. The seed is much smaller than in *P. montanus*, has a cylindrical spine-like crest, and is borne on a specialized reproductive branch which has only scales rather than foliar leaves. Compare figs. 32 and 33 with figs. 24 and 25. The leaves of *P. Standleyi* become much larger and are very glaucous beneath. (fig. 34).

* Named in honor of Paul C. Standley, Curator of the Herbarium, Chicago Natural History Museum, in recognition of his outstanding contributions to our knowledge of the flora of Costa Rica.

LITERATURE CITED

1. BERTRAND, C. E. Anatomie Comparée des Tiges des feuilles chez les Gnétacées et les Conifères. Ann. des Sci. Nat. ser. V. 20: 5-153. 1874.
2. BUCHHOLZ, J. T. Embryogeny of the Podocarpaceae. Bot. Gaz. 103: 1-37. 1941.
3. DU TOIT, ALEX. L. Our wandering continents. Edinburgh and London. 1937.
4. ENGLER, A. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, Nachträge zu II-IV, p. 21. 1897.
5. FLORIN, R. Untersuchungen zur Stammesgeschichte der Coniferales u. Cordaitales. Erster teil. Morphologie und Epidermisstruktur der Assimilationsorgane bei den rezenten Koniferen. Svenska Vet.-Akad. Handl. ser. 3, 10. Stockholm. 1931.
6. ———. Die Koniferen des Oberkarbons u. des unteren Perms. Palaeontographica 85 (B1-7): 1938-1944.
7. FULLING, EDMUND H. Identification, by leaf structure, of the species of *Abies* cultivated in the U. S. Bull. Torrey Bot. Club 61: 497-524. 1934.
8. GRIFFIN, E. M. Conifer leaves with regard to transfusion tissue and to adaptation to environment. Transactions of the New Zealand Institute 40: 43-72. 1907.
9. LANJOUW, J. On the standardization of herbarium abbreviations. Chronica Botanica, 5: 142-150. 1939.
10. MAHLERT, ADOLPH. Beiträge zur Kenntnis der Anatomie des Laubblätter der Coniferen mit besonderer Berücksichtigung des Spaltöffnungs-Apparates. Bot. Centralbl. 24: 54-59, 85-88, 118-122, 149-153, 180-185, 214-218, 243-249, 278-282, 310-312. 1885.
11. ORR, M. Y. The leaf anatomy of *Podocarpus*. Trans: Proc. Bot. Soc. Edinburgh 34 (1): 1-54. 2 plates. 1944.
12. PILGER, R. Taxaceae. Engler Pflanzenr. IV. 5 (Heft 18): 1903.
13. ———. Coniferae. Nat. Pflanzenfam. ed. 2, 13: 1926.
14. WASSCHER, J. The genus *Podocarpus* in the Netherlands Indies. Blumea 4: 359-481. 1941.
15. WILDE, MARY L. A new interpretation of coniferous cones. I. Podocarpaceae. Ann. Bot. n.s. 8: 1-41. 1944.
16. WORSELL, W. C. On "transfusion tissue": its origin and function in the leaves of gymnospermous plants. Trans. Linn. Soc. (Second series) 5: 301-319. 1897.

EXPLANATION OF FIGURES

All photomicrographic illustrations of leaf sections for this investigation were made from unstained leaf sections cut free hand from the leaves of herbarium specimens, mounted in glycerine. Figures 11 and 12 showing the presence and absence of the Florin ring (Fl) are exceptions which were removed after maceration and stained with safranin, mounted in balsam, outer side up and photographed under high magnification.

SYMBOLS: *e*, epidermis; *h*, hypoderm; *sc*, sclerid; *p*, palisade tissue; *r*, resin canal; *tr*, transfusion tissue; *act*, accessory transfusion tissue; *Fl*, Florin ring.

PLATE I

FIG. 1. *Podocarpus Cummingii* Parl. R. M. Holman 0004 (DS). Transverse section of leaf showing epidermis and hypoderm interrupted by stomates on both sides of leaf. This leaf is flattened vertically and has stomates in rows of 2-5 on 4 sides. Resin canal (*r*) beneath vascular bundle is large, bundle has a very small amount of transfusion tissue at the right and left and there is no accessory transfusion tissue. $\times 48$.

FIG. 2. *Podocarpus amarus* Blume. C. E. Lane-Poole s.n. (A). Transverse section of central portion of leaf, showing absence of hypoderm with palisade layer abutting heavily cutinized epidermis. The large vascular bundle shows well developed transfusion tissue (*tr*) and accessory transfusion tissue (*act*), the latter extending to the margin of the leaf.

The air chambers found below near the resin canal (*r*) might be confused as additional resin canals, which our sections have usually shown to be single. Stomates are confined to lower (abaxial) surface. $\times 48$.

FIG. 3. *Podocarpus falcatus* (Thunb.) R.Br. Whitford 27 (US). Transverse section of leaf showing epidermis and hypoderm (*h*) interrupted above and below except at margins and midvein, with large wing-like expansions of transfusion tissue (*tr*) extending nearly halfway to leaf margin but without traces of accessory transfusion tissue. Vascular sclerids are shown above and below bundle and a single resin canal (*r*) near phloem. Stomates are equally distributed on both sides of leaf. $\times 48$.

FIG. 4. *Podocarpus Rospiigiosii* Pilger. Archer 541 (US). Transverse section of lower portion of half of leaf, showing epidermis and interrupted hypoderm. There are stomates on both sides of leaf. The vascular bundle with 3 resin canals (*r*) below, shows (as in FIG. 3) wing-like expansions of transfusion tissue (*tr*) and is likewise without accessory transfusion tissue. $\times 48$.

FIG. 5. *Podocarpus elongatus* L'Herit. Transverse sections of midvein and half of leaf showing epidermis (*e*), hypoderm (*h*) continuous above, interrupted below where the stomates are found. Vascular bundle shows a single resin canal with well developed vascular sclerids below phloem. Transfusion tissue (*tr*) is found on each side of vascular bundle; accessory transfusion tissue (*act*) extends toward margin of leaf where a marginal resin canal (*r*) may be seen. $\times 48$.

FIG. 6. *Podocarpus Totara* D. Don. R. J. Matthews s.n. (UC). Transverse section of half of leaf showing continuous hypoderm above, interrupted below, where the stomates are found. The palisade tissue is developed only on upper side. There are no accessory sclerids of any kind; resin canal (*r*) is single near vascular bundle; transfusion tissue (*tr*) is present at left and right of bundle but no accessory transfusion tissue is present; instead the mesophyll cells are slightly elongated. $\times 48$.

PLATE II

FIG. 7. *Podocarpus montanus* var. *meridensis* Buchh. & Gray. Klugh s.n. (Ven). Transverse section of central portion of leaf showing epidermis, absence of hypoderm, and well developed palisade tissue bordering directly upon epidermis. Stomates are confined entirely to lower surface of leaf. Vascular bundle has no sclerids; has only small areas of transfusion tissue (*tr*) and no accessory transfusion tissue or sclerids of any kind. This leaf has a groove above midvein, much more open in this variety than in most leaves of the *montanus* group. $\times 48$.

FIG. 8. *Podocarpus macrophyllus* (Thunb.) D. Don. Cult. Jamaica. Transverse section of central portion of leaf showing hypoderm above and below, interrupted above where there are no stomates and absent below except at leaf margin and beneath midvein. Vascular bundle with transfusion tissue (*tr*) and well developed accessory transfusion tissue (*act*) which extends to margin of leaf. There are three resin canals (*r*) beneath vascular bundle but no vascular sclerids or other accessory sclerids. $\times 48$.

FIG. 9. *Podocarpus oleifolius* (?) Steyermark 53431. Transverse section of leaf at one side of vascular bundle, showing epidermis and continuous hypoderm above (at right) interrupted hypoderm below (at left) where stomates are confined, and accessory transfusion tissue (*act*) at center. The palisade tissue shows several palisade and accessory sclerids (*sc*) in mesophyll below palisade layer. $\times 48$.

FIG. 10. *Podocarpus nubigenus* Lindl. C. Junger 73 (Mo). Transverse section near vascular bundle showing hypoderm continuous above, below only at midvein and interrupted elsewhere below where stomates occur; a single resin canal (*r*) beneath vascular bundle, with transfusion tissue on each side but no accessory transfusion tissue. In the position of the latter several large sclerids (*sc*) are shown. $\times 48$.

FIG. 11. *Podocarpus oleifolius* (?) Steyermark 53431. Part of lower epidermis after maceration stained and mounted under high magnification, showing the Florin ring (*Fl*) a thin furrow giving a non-staining circle in the cuticular layer above subsidiary cells. $\times 212$.

FIG. 12. *Podocarpus novae-caledoneae* Vieill. Franc 96 (LA). Lower epidermis, same treatment as FIG. 11 showing absence of Florin ring. $\times 212$.

FIG. 13. *Podocarpus Harmsianus* Pilger. Fendler 1289 (Ph.). Specimen from lectotype collection showing leaves with ridge above midvein. $\times 2/3$.

PLATE III*

Figs. 14–16. *Podocarpus utilior* Pilg. Figs. 14 and 15 parts of photograph of type specimen Weberbauer 2114 (F) enlarged to natural size. FIG. 16 Soukup 1802 (III) bearing female cones.

FIG. 17. *Podocarpus Harmsianus* Pilg. Viereck in Dec. 1922 (US) showing female cones and numerous ovules near time of pollination, mature seeds and leaves with ridge above midvein.

FIG. 18. *Podocarpus montanus* (Willd.) Lodd. I. F. Holton in 1854 (NY) showing leaves with groove above midvein and spicate arrangement of pollen cones.

FIG. 19. *Podocarpus montanus* var. *meridensis* Buchh. & Gray. Steyermark 57103 type (III.) Leaves have groove above midvein (lower sides shown here) and seeds borne at ends of leafy branches.

PLATE IV*

FIG. 20. Logging operations at Oxapampa, Peru, showing very large trees, presumably *P. utilior* Pilg. Photo. supplied by J. Soukup.

Figs. 21–23. *Podocarpus Harmsianus* Pilg. FIG. 21 Jahn s.n. (US). Nor Leon (near Tovar in Aragua) female cones past time of pollination with ovules dropped away, only one subterminal ovule remaining, the special branch having scale leaves. FIG. 22 Tamayo 1575 (Ven.) from a cultivated specimen, at Tovar in Aragua (type locality) showing crestless seed appearing terminal, actually sub-terminal. This twig exposes lower sides of leaves. FIG. 23 Viereck in Dec. 1922 (US) from Colombia for comparison with FIG. 8.

Figs. 24–25. *P. montanus* (Willd.) Lodd. FIG. 24 Steyermark 54472 (III) from Ecuador near Loja showing large leaves with groove above midvein, fruiting branch with seed in terminal position and detached seeds.

FIG. 25. Seeds with flat crests, same collection (F).

FIG. 26. *Podocarpus andinus* Poeppig. Seeds from packet of Phillipi in 1888 (NY).

Figs. 27–31. *Podocarpus montanus* var. *densifolius* (Kunth) Buchh. & Gray.

FIG. 27. Purdie s.n. (NY) showing leafy reproductive branch bearing 2 double crested ovules and a full grown seed with 2 distinct blunt crests.

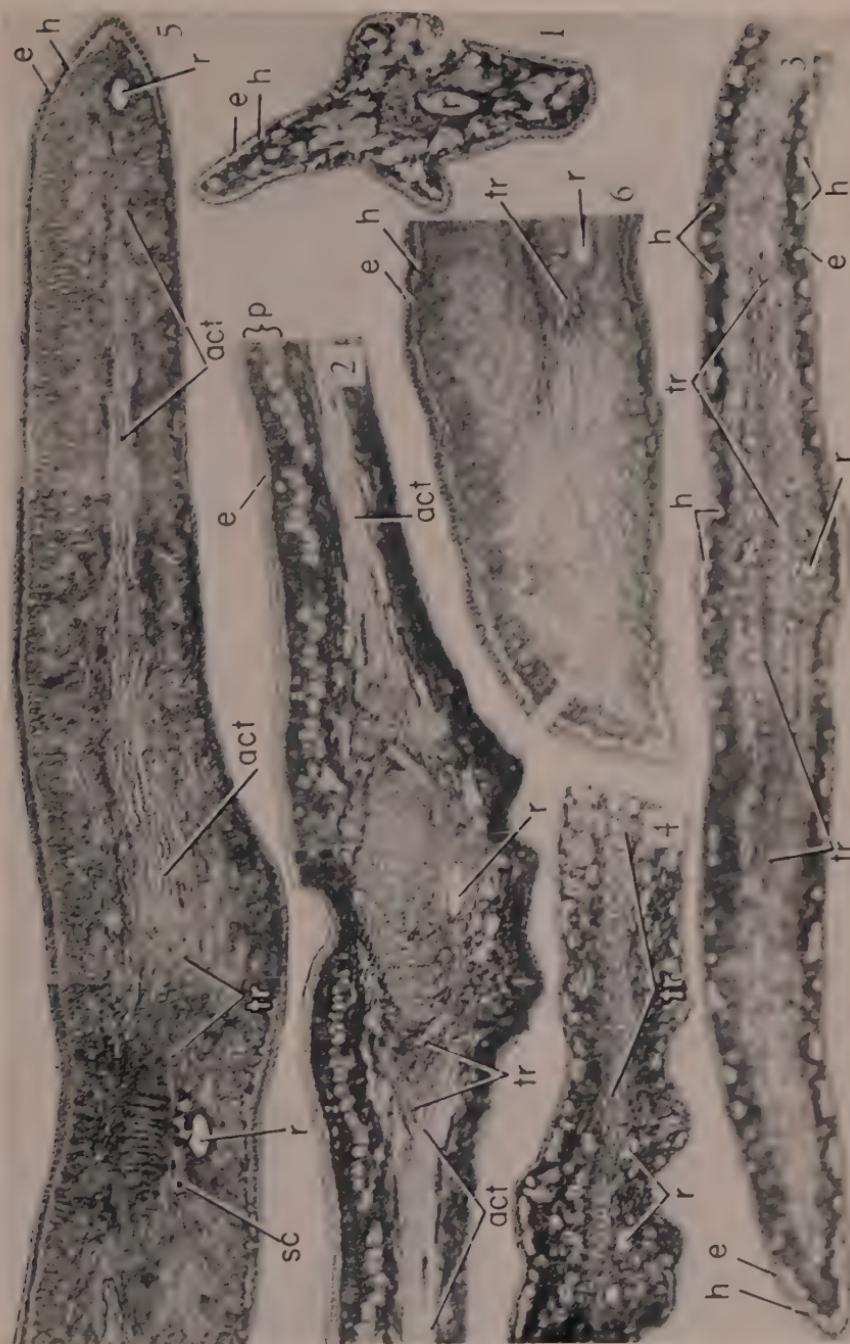
FIG. 28. Pennell 2436 (NY) showing foliage. Seeds from western Venezuela.

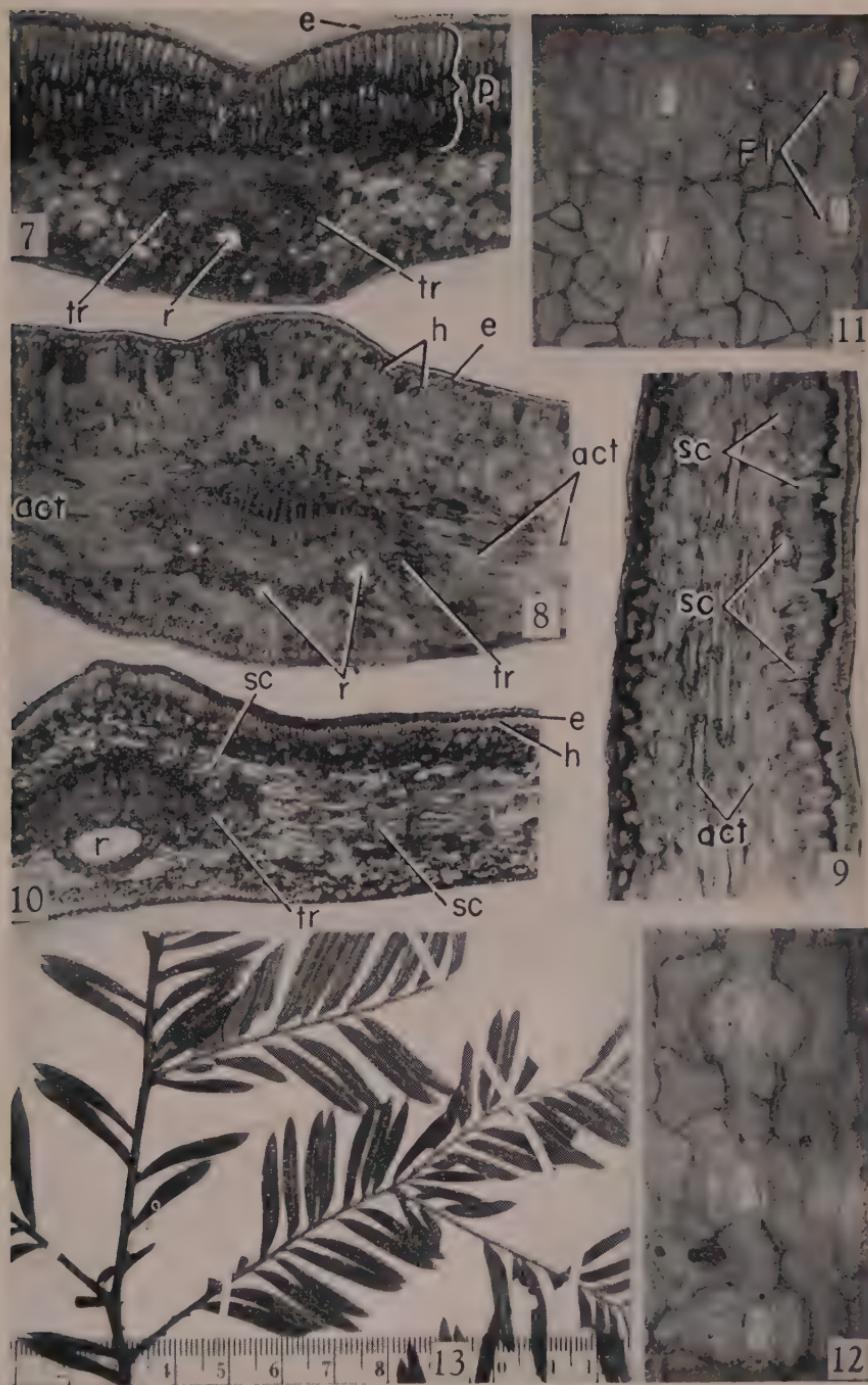
*All figures 7/8 natural size.

FIG. 29. *Delgado* 366 (Ven.). FIG. 30 *Klugh* (Ven.). FIG. 31 *Steyermark* 57103.

FIGS. 32-34. *Podocarpus Standleyi* Buchh. & Gray. FIG. 32 *Tonduz* 10743 (US) showing leaves and female cone, clothed with scales rather than leaves. FIG. 33 *Tonduz* 10333 type (US), seed with crest and conical cylindrical spine. FIG. 34 *J. D. Smith* 6857 (US) showing large leaves with lower surface glaucous.

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MORPHOLOGY AND RELATIONSHIPS
OF
ILLICIUM, SCHISANDRA AND KADSURA
I. STEM AND LEAF

I. W. BAILEY AND CHARLOTTE G. NAST

With six plates

INTRODUCTION

IN A PREVIOUS PAPER (1), we called attention to the fact that plants of general ranalian affinities may be divided upon the basis of their pollen morphology into two major categories, viz. (1) those resembling many monocotyledons in having monocolpate pollen or pollen phylogenetically derived from such types of microspores and (2) those resembling most dicotyledons in having tricolpate or derived types of pollen. All plants of the former category, with the exception of the aquatic Cabomboideae and Nymphaeoidae, have secretory cells of a fundamentally similar type. Such "resin" or "ethereal oil" cells do not occur in the second category of ranalian plants, except in *Illicium*, and the Schisandraceae. The secretory idioblasts of *Tetracentron* are of a different morphological type, being elongated and not infrequently ramified.

Since *Illicium*, *Schisandra* and *Kadsura* exhibit evidences of relationship to both major categories of ranalian plants and may prove to be significant in future discussions of the phylogeny of the dicotyledons, it is desirable that the three genera be re-examined from a broad morphological point of view. Material recently assembled by our colleague, Dr. A. C. Smith, for taxonomic revisions of *Illicium* and the Schisandraceae, has provided accurately identified specimens for such investigations. We have examined 34 of the 42 species of *Illicium*, 22 of the 25 species of *Schisandra*, and all of the 22 species of *Kadsura* recognized by Dr. Smith (9).

STEM: XYLEM

The young stem of *Illicium* is characterized by its unilacunar nodes, each leaf having at its base an arc-shaped strand of vascular tissues that is related to a single broad parenchymatous lacuna in the vascular cylinder of the vegetative axis, *Fig. 1*. The later-formed primary vascular elements of the internodal parts of the stem — in contrast to those of the Degeneriaceae, Himantandraceae, Magnoliaceae, Winteraceae, *Trochodendron*, *Tetracentron*, and *Euptelea* — are not aggregated in discrete bundles that are separated by conspicuous parenchymatous, interfascicular parts. The primary xylem tends to be more or less loosely and uniformly dis-

tributed in a pseudo-siphonostelic rather than in a typically eustelic-appearing arrangement.

The rays of the first-formed secondary xylem are uniserial, vertically extensive and composed of "upright" cells, *Fig. 9*. Subsequently, certain of the ray initials of the cambium divide anticlinally, leading in later-formed wood, *Fig. 10*, to the transformation of parts of the original uniserial rays into low, biserial, triserial or occasionally quadriseriate rays in which the long axis of the constituent cells is radially instead of vertically oriented, compare *Figs. 7* and *10*. Thus, the wood of older stems, in contrast to that of ordinary herbarium specimens, is characterized by having a typically "heterogeneous" type of ray structure. As demonstrated by Kribs (8) and Barghoorn (2), a commonly occurring trend of structural specialization in dicotyledons involves reduction or elimination of multiserial rays. In *Illicium*, this trend of specialization has progressed to a level where multiserial rays are eliminated from the first-formed secondary xylem and are reduced in width and height in the later-formed wood. The distribution of the wood parenchyma is transitional between diffuse and scanty abaxial paratracheal, *Fig. 7*.

Although the rays and the wood parenchyma of *Illicium* exhibit conspicuous evidences of phylogenetic modification, the tracheary elements are of relatively primitive types. The long, slender, thin-walled, angular vessel members have extensively overlapping ends with numerous bars in their scalariform perforation plates. The pitting between vessels, and between vessels and parenchyma, is scalariform with transitions to opposite-multiseriate. The imperforate tracheary elements have conspicuous bordered pits and are essentially thick-walled tracheids from a morphological point of view. The vessels are diffusely distributed throughout the secondary xylem, pore multiples being of infrequent or sporadic occurrence. Where growth layers are clearly differentiated in the secondary xylem, the vessels of the earlywood may be somewhat larger than are those of the latewood, *Fig. 7*.

The young stems of *Schisandra* and *Kadsura* have unilacunar nodes, but differ from those of *Illicium* in forming tripartite foliar traces, *Fig. 4*. The internodal parts of the stems exhibit a wide range of variability both in the arrangement of the primary xylem and in the detailed structure of the secondary wood. In certain of them, *Fig. 14*, the primary xylem occurs in relatively widely spaced strands, i.e., in a typically eustelic arrangement; whereas in others, *Fig. 13*, the vessels of the last-formed primary xylem appear as a continuous ring, i.e., in transverse sections of the internode.

The secondary xylem may be dense and of a relatively primitive structural type, *Fig. 14*, or it may be of a highly specialized and extremely porous type such as occurs commonly in many scandent plants, *Fig. 8*. The first-formed secondary xylem frequently is of the former type, transition to increasing porosity occurring during subsequent stages of the enlargement of the stem, *Fig. 14*. In other cases, the cambium first forms a narrow zone of nearly vesselless xylem which is succeeded by an abrupt

and precocious transition to a conspicuously porous type of wood, *Fig. 13*. Certain stems exhibit more or less clearly defined zones of alternating density and porosity.

As indicated in *Fig. 14*, the inner zones of unmodified secondary xylem are characterized by having slender diffusely scattered vessels, thick-walled tracheids, multiseriate rays that extend outward from the interfascicular parts of the eustele and numerous intervening high-celled uniseriate rays. The distribution of wood parenchyma is scanty diffuse and abaxial paratracheal. Such secondary xylem—allowing for differences due to its ontogenetic position—resembles the wood from older stems of *Illicium*, compare *Figs. 7* and *14*, but a majority of its vessels differ from those of *Illicium* in having a reduced number of bars and enlarged openings in their scalariform “perforation plates.” Vessel members exhibiting early stages of their phylogenetic derivation from scalariformly pitted tracheids are, however, of not infrequent occurrence. In contrast to this relatively primitive type of secondary xylem, the highly specialized porous type of wood illustrated in *Fig. 8* is characterized by its huge vessels, its large, thin-walled, profusely pitted tracheids, and its more abundantly developed paratracheal parenchyma. In structurally more specialized stems, the rays of the first-formed secondary xylem are prevailingly uniseriate, *Fig. 13*, certain of them subsequently broadening to multiseriate rays. The larger vessels have perforation plates with a single large circular or oval opening. The pits between such vessels and parenchyma are conspicuously enlarged, having large apertures and more or less vestigial borders on the vessel side. Where vessels are in contact, the pitting is scalariform or transitional to opposite. Alternating seriations of bordered pits occur at times between vessels and tracheids.

It is evident, accordingly, that the xylem of *Illicium* is of a relatively uniform and stable type. On the contrary, the wood of *Schisandra* and *Kadsura* exhibits a wide range of structural variability, as is so commonly the case in scandent plants. Conspicuous structural differences occur not only in stems of different species, but also in different stems from presumably the same species and even in different shoots of the same plant. A wealth of specially collected material must be examined before it will be possible to determine the exact significance of anatomical criteria in differentiating species and varieties. Such intensive investigations of the scandent schisandras and kadsuras should prove, however, to be extremely significant from both morphological and physiological points of view.

STEM: PHLOEM

In addition to rays, the recently formed phloem of *Illicium* consists of numerous contiguous sieve tubes among which are scattered companion cells, phloem parenchyma strands and cambiform cells of a special type. The long, slender sieve tube members have extensively overlapping ends with numerous, often widely separated, sieve areas. The cells of the rays and of the parenchyma strands have large vacuoles that contain a high

ratio of tannin or other phenolic compounds. The cambiform cells have layered "mucilaginous" contents which expand rapidly in water and stain intensely with ruthenium red. As a stem increases in diameter, sclereids tend to be formed sooner or later in the older, outer secondary phloem. These more or less ramified stone cells may be diffusely scattered or they may be aggregated in compact masses of varied form. Slender, thick-walled fibres are confined to the primary body and when present in the stem are diffusely scattered about the outer periphery of the stele in the so-called pericyclic zone.

The phloem of *Schisandra* and *Kadsura* resembles that of *Illicium* in containing numerous elongated or cambiform elements with stratified "mucilaginous" contents. The "mucilage cells" of the first-formed phloem commonly tend to become more or less extensively dilated, *Fig. 12*, in contrast to those of the subsequently formed secondary phloem which retain a more slender form, as in the phloem of *Illicium*.

There is a more precocious development of sclerenchyma in the secondary phloem of *Schisandra* and *Kadsura* than in homologous tissue of *Illicium*, and the more or less extensively clustered, thick-walled, lignified elements are of an entirely different morphological type. In contrast to the ramified stone cells of *Illicium*, the sclerenchymatous elements of *Schisandra* and *Kadsura* are of a linearly elongated and fiberlike form, *Fig. 26*. As noted by Solereder (10), the thick, lamellated, unpitted secondary wall of these cells develops asymmetrically, gradually crowding the protoplast laterally toward the periphery of the cell, *Fig. 23*. During the last stages of secondary wall formation, numerous crystals of calcium oxalate become encysted in the outer surface of the cellulose adjacent to the constricted protoplast. This asymmetry in the development of the secondary wall and in the distribution of crystals occurs characteristically in the sclerenchymatous elements of all species of *Kadsura* and *Schisandra*. As will be shown on subsequent pages, diversified forms of this crystal-bearing sclerenchyma occur more or less abundantly in the cortex and pith of the stem, in the leaf and the flower, and thus are a significant diagnostic characteristic of the Schisandraceae.

"Pericyclic" fibers are more abundantly developed in the Schisandraceae than in *Illicium*. They differ markedly from the crystal-bearing sclerenchymatous elements of the secondary xylem, having normal symmetrically developed walls, and being conspicuously pitted and septate. They commonly appear as a more or less continuous zone or ring in cross sections of young stems. However, this ring of "pericyclic" fibers becomes disrupted into disconnected arcs or strands during subsequent enlargement of the stem. Not infrequently the earlier breaks in the "pericyclic" ring become occluded by crystal-bearing sclerenchymatous elements of bizarre forms.

STEM: CORTEX AND PITH

Three types of idioblasts are of more or less frequent occurrence in the cortex and pith of *Illicium*. Globular "resin" or "ethereal oil" cells,

having a tenuous "suberized" inner membrane which stains in Sudan IV, occur commonly in the cortex. They vary considerably in size and number. "Mucilage" cells of diversified size and form and of fluctuating abundance may be formed in both the cortex and the pith. More or less conspicuously branched sclereids occur at times in the cortex or in both the cortex and the pith.

The cortex and the central part of the pith are badly collapsed in most herbarium specimens of *Schisandra* and *Kadsura*, and, therefore, are poorly preserved for anatomical investigations. It is evident, however, that globular "ethereal oil" cells are of common occurrence in the cortex, *Fig. 12*, and that "mucilage" cells frequently are present in the succulent central core of the pith. Furthermore, crystal-bearing sclerenchymatous elements are formed in the cortex and not infrequently in the pith. These cells fluctuate widely in size, form, and number in different stems. They may be abundantly developed throughout the cortex and pith of the internodal parts of the stem or they may be few in number and confined to the nodal parts.

LEAF: EPIDERMIS AND STOMATA

Throughout the genus *Illicium* the lateral walls of the lower epidermis, as seen in surface view of the leaf, are conspicuously pitted and undulating, *Fig. 11*. It should be noted in this connection, however, that drying and reagents which tend to contract the epidermis may accentuate the undulations, whereas treatments that excessively reexpand the cells and cell walls reduce or eliminate the wavy outlines. The lateral walls of the upper epidermis may be either smooth or undulating.

The cuticle of the under surface of the leaf is commonly characterized by having parallel, ridge-like thickenings. These projections of the outer surface of the cuticle, *Fig. 11*, may be coarse and conspicuous or very fine and easily obscured in preparing leaves for microscopic examination. They are distributed in specific patterns, e.g., oriented parallel to the long axis of the mid-rib and the larger veins, concentrically about the stomata and radially in the rosettes of cells surrounding the secretory cells of the lower epidermis, *Fig. 11*. They may be uniformly distributed, or confined to restricted areas, viz. about the stomata, the secretory cells, or the larger veins. Ridge-like thickenings of the cuticle may occur also on the upper surface of the leaf.

According to Solereder (10), the stomatal guard cells of *Illicium Griffithii* (?) and *I. religiosum* (?) have lobe-like appendages that are oriented along extensions of the major axis of the aperture. Similar structural appearances occur in nearly all of the 73 collections of *Illicium* examined by us and, therefore, are characteristic of the genus. When the lower epidermis is examined unstained in surface view, the stomata exhibit a deceptive, superficial resemblance to those of Gramineae, see Haberlandt (7), where the guard cells are shaped like dumb-bells, having dilated thin-walled ends connected by a slender very thick-walled part. The lobe-like

appearances are also suggestive of the lightly cutinized polar areas in Bennettitalean stomata, see Florin (5).

That the stomatal apparatus of *Illicium* is actually of a fundamentally different type may be demonstrated, however, by examining strips of the epidermis and thin transverse sections of the leaf that have been stained with Sudan IV.¹ In such preparations, the hypothetical lobe-like appendages prove to be tapered, intercellular intrusions of the cuticle between the constricted ends of the guard cells, compare *Figs. 16 and 17*. When the stomatal apparatus is examined in surface view at upper focal levels, these intrusions are seen to be in continuity with broad arcs of cutin which project inward between the guard cells and adjacent epidermal cells, the combined cuticular intrusions resembling a head with a broad-brimmed hat, *Fig. 17*. These intercellular intrusions of the cuticle fluctuate considerably in form as seen in surface and sectional views, but tend to be massive except in *I. floridanum* Ellis and certain collections of *I. parviflorum* Michaux, where they are reduced to tenuous wedges of cutin. In surface view, the outlines of the paired guard cells vary from narrowly to broadly elliptical, the dimension of the major axis fluctuating from 30 to 70 microns with corresponding variations in the minor axis. Each pair of guard cells is accompanied by 2 to 4 subsidiary cells oriented parallel to them, *Fig. 17*. These subsidiary cells appear to have been derived from the same mother cell as the guard cells. Subsidiary cells that are adjacent to guard cells tend to broaden internally and to underlie the guard cells, *Figs. 15 and 17*. Occasionally the internal expansion is so extensive that the subtending parts of the subsidiary cells become concrescent, thus sealing the stoma internally. Where two subsidiary cells are formed lateral to a guard cell, *Fig. 17*, the one adjacent to the guard cell frequently has a narrow exposed outer surface. In certain cases, so little of the cell is exposed that it is easily overlooked in surface view except under high magnification.

Most leaves of *Illicium* have comparatively thick cuticles within which a conspicuous vestibule or entrance to each stoma is formed, *Fig. 15*. The size and form of this cuticular vestibule fluctuate widely, not only in different collections of *Illicium*, but also in different parts of the same leaf. The outer aperture of the vestibule may be large or small, narrowly or broadly elliptical, or more or less rectangular in surface view, due in part to variations in the form and the extension of the outer rim-like projection

¹ Strips of cuticle with attached epidermal cells were obtained by macerating pieces of leaf in a mixture of equal volumes of 5% chromic and 5% nitric acids at a temperature of 56° C. These were then washed, stained in Sudan IV and mounted in glycerine. If the macerating treatment is unduly prolonged, the cuticle is modified and loses its staining capacity in Sudan IV.

Sections of leaves were prepared by soaking pieces of the lamina in hot water, then in either warm (45° C.) lactic acid or glycerine for two days. The pieces of leaves were then washed, dehydrated, embedded in paraffin, serially sectioned, bleached in concentrated hydrogen peroxide, stained in Haidenhain's haematoxylin and Sudan IV and mounted in glycerine.

of the cuticle, *Fig. 15*. There is also more or less extensive internal cutinization subtending the guard cells. The rim-like projections of these cutinized parts commonly are in contact in closed stomata, whereas the walls of the guard cells are not.

In contrast to the tough, leathery, entire leaves of *Illicium*, those of *Schisandra* and *Kadsura* are softer, thinner and commonly provided with more or less numerous serrations. The lateral walls of the epidermal cells may be conspicuously pitted and undulating, but these characters are less pronounced and constant than they are in most species of *Illicium*. Although the cuticle is in general much thinner, it frequently exhibits a more or less conspicuous ribbing which closely resembles that which occurs so conspicuously in *Illicium*. There is a similar radial pattern in the rosettes of cells that surround the secretory cells of the lower epidermis. Furthermore, there are at times similar, but less massive, intrusions of cutin between the ends of the guard cells, *Figs. 18 and 19*. In such cases, there usually are no intrusions of cutin between the ends of the guard cells and adjacent epidermal cells, such as occur so characteristically in the stomatal apparatus of *Illicium*, *Fig. 17*.

The stomata are relatively large, the outline of the paired guard cells fluctuating between narrowly and broadly elliptical and having as in *Illicium* a major axis of from 30 to 70 microns. The subsidiary cells of the stomatal apparatus fluctuate widely in size, form, number and arrangement even within the limits of a single leaf. At one extreme are stomata that have subsidiary cells oriented parallel to the guard cells, as in *Illicium*, *Fig. 17*. At the other extreme of structural variability are guard cells that are subtended by parts of ordinary epidermal cells of diversified form. Numerous transitions between these structural extremes are of common occurrence, *Figs. 18 and 19*. Whether all or certain of the subsidiary cells are derived from the same primordial cell as the guard cells can be determined only by detailed ontogenetic and cytological investigations.

LEAF: VASCULARIZATION

The leaves of *Illicium* are characterized by having a simple, arc-shaped strand of vascular tissues that extends throughout the petiole and the mid-rib of the lamina, *Figs. 1-3*. On the contrary, the leaves of *Schisandra* and *Kadsura* usually have three discrete strands of vascular tissues in the petiole, *Fig. 5*, and the basal part of the lamina. The three separate bundles are replaced, however, by a single arc with involute margins in the central and apical parts of the lamina, *Fig. 6*. Occasionally aberrations occur in this typical pattern of vascularization. In certain cases, the three strands of primary vascular tissue may be bridged by cambial activity. Conversely, division may occur at times, giving rise to more than three strands in the petiole.

LEAF: IDIOBLASTS

Three types of idioblasts, viz. "resin" cells, "mucilage" cells and ramified sclereids, may be present in the leaf, as in the stem, of *Illicium*.

No sclereids are present in the lamina of 30 of the 73 collections of this genus examined by us. In 22 cases, they are diffusely distributed throughout the mesophyll, whereas in 21 of the collections they are confined to tissue in close proximity to the mid-rib. Sclereids occurring in the more spongy parts of the mesophyll tend to be profusely ramified and of highly diversified forms. The lumen may be relatively large and the branches conspicuously tapered, *Fig. 20*, or the lumen may be vestigial and the branches nearly cylindrical with blunt apexes, *Fig. 21*. Sclereids in close proximity to the mid-vein and the vascular tissue of the petiole frequently tend to be massive, to have rectangular outlines in sectional views, and to be provided with contorted branches or with broad irregular lobes, *Fig. 22*. The foliar sclereids of *Illicium* differ from those of *Trochodendron*, see Foster (6), in their smaller size, their less extensive branching and in having smooth, rather than spiculate, outer surfaces.

It should be noted in these connections that the mid-vein and the larger lateral veins usually have a coating of slender, thick-walled fibres, comparable to the "pericyclic" fibres of the stem. Such fibres do not occur, however, about the terminal veinlets which are entirely devoid of sclerenchymatous elements, except in one collection of *I. majus* Hook.f. and Thomson, *Lau* 28772. "Pericyclic" fibres may be present or absent in the petiole.

The foliar "ethereal oil" or "resin" cells of *Illicium* fluctuate considerably in size and abundance. They tend to occur in the spongy mesophyll and the lower epidermis, and to be infrequent, if not invariably absent, in palisade tissue and the upper epidermis. Although they usually are spherical or ovoid in form, they may at times become somewhat lobate in tissue having large intercellular lacunae. Those that originate in the lower epidermis expand inwardly among the subepidermal cells of the leaf. As previously stated, their exposed outer part forms the center of a characteristic rosette of radially oriented epidermal cells, *Fig. 11*.

The size, form and distribution of "mucilage" cells should be studied in freshly collected leaves from living plants, dried leaves from herbarium specimens being unfavorable material for this purpose. In many cases, these cells appear to be confined to the palisade tissue, as observed by Blenk (3) in three species of *Illicium*.

The foliar "ethereal oil" cells of *Schisandra* and *Kadsura* resemble those of *Illicium* in general size, form and distribution, those of the lower epidermis forming the center of similar rosettes of radially oriented epidermal cells. The vascular strands of the petiole and the veins of the lamina differ, however, from those of *Illicium* in having conspicuous and more or less extensively dilated "mucilage" cells of elongated form in the primary phloem (darkly stained cells in *Figs. 5* and *6*). The leaves of *Schisandra* and *Kadsura* also differ markedly from those of *Illicium* in the character and the distribution of sclerenchymatous elements. Typical pitted, symmetrically thickened and profusely ramified sclereids do not occur in the former genus. As in the case of the stem, the sclerenchymatous elements

of the leaf are of an unpitted, asymmetrically thickened and crystal-bearing type. They fluctuate widely in size, form and distribution, *Figs. 24-29*.

In the sections *Pleiostema*, *Maximowiczia* and *Euschisandra* of *Schisandra* and in the section *Cosbaea* and part of the section *Sarcocarpon* of *Kadsura*² crystal-bearing sclerenchyma is absent in the lamina and is confined to the basal part of the petiole. In these plants, such cells are usually absent in the pith of the internodal parts of the stems. On the contrary, in the section *Sphaerostema* of *Schisandra* and in the section *Eukadsura* and part of the section *Sarcocarpon* of *Kadsura*, crystal-bearing sclerenchyma occurs, not only in the petiole, but also in the lamina of the leaf. In most cases, the more or less elongated crystal-bearing elements are scattered along the vascular bundles, veins and veinlets, with their long axis oriented parallel to that of the vascular elements. There are, however, several species in the section *Sarcocarpon* of *Kadsura* which exhibit conspicuous aberrations. In *K. marmorata* (E. G. and A. Henderson) A. C. Sm., *Elmer* 11718, *K. lanceolata* King, *M. R. Henderson* 11562, *K. borneensis* A. C. Sm., *J. and M. S. Clemens* 31889, and *K. Clemensiae* A. C. Sm., *J. and M. S. Clemens* 22115 (type), the crystal-bearing elements either are oriented at right angles to the veins or their elongated ends protrude freely into the mesophyll. In *K. marmorata*, some of these sclerenchymatous cells occur independently in the mesophyll and are not related in development to the veins.

The form and the distribution of ordinary pitted fibers are less stereotyped in leaves of *Schisandra* and *Kadsura* than they are in the foliar organs of *Illicium*. The veins and the terminal veinlets may be heavily jacketed by such elements or they may be devoid of them. Not infrequently short fibrous elements are scattered along the veins much as are the elongated crystal-bearing cells. Particularly in the section *Sarcocarpon* of *Kadsura*, there are transitions from elongated fibrous elements to short, broad, irregularly shaped, pitted cells that jacket the terminal veinlets.

DISCUSSION

Illicium obviously is a genus that exhibits a number of relatively stable structural characters in its vegetative organs. Particularly significant in this connection are the uniformity of its unilacunar nodal anatomy, the characteristic vascularization pattern of its leaf, the pseudo-siphonostelic rather than typically eustelic-appearing arrangement of its primary vascular tissues, the specific combinations of primitive and specialized anatomical features of its secondary xylem and phloem, and the curious intercellular intrusions of the cuticle in its stomatal apparatus.

In contrast to *Illicium*, *Schisandra* and *Kadsura* exhibit a combination of relatively stable and highly variable anatomical characters. On the one hand, there is considerable uniformity in the nodal anatomy, the vascularization pattern of the leaf, the presence of conspicuously dilated

² For lists of the species included in these sections see Smith (9).

"mucilage" cells in the primary phloem, and the occurrence of curious, asymmetrically thickened, crystal-bearing elements, particularly in the secondary phloem. On the other hand, there is a wide range of variability in the structure of the stomata and especially in the vascular tissues of the stem. The xylem fluctuates—even within the limits of a single plant—from a relatively primitive type to extremes of structural specialization.

What conclusions may be deduced from such anatomical data regarding the affinities of the three genera? How should the various anatomical criteria be weighed in so doing? What actually are the merits of including these genera within the Magnoliaceae? Significant answers to these questions must be based upon a broad knowledge of the behavior of anatomical characters in a wide range of dicotyledonous families. Due allowances must be made for commonly occurring structural similarities due to parallel or convergent evolution, and for differences due to excessively divergent trends of morphological specialization in plants of certain habits of growth, e.g., vines.

During the last 30 years, extensive investigations of the vascular tissues in all of the principal orders and families of the dicotyledons have revealed and clarified the salient trends of phylogenetic specialization that occur in these tissues. Thus, it now is possible in many cases to assess the evolutionary significance of specific combinations of structural characters in the vascular tissues. Unfortunately, there is as yet no comparable body of reliable information regarding the epidermis, cortex and pith of the stem and the epidermis and mesophyll of the leaf in dicotyledons. Therefore, there is no conclusive evidence available at present for determining whether the ancestral dicotyledons actually possessed certain specific types of stomata, secretory cells, sclerenchyma, etc.

The vegetative organs of *Schisandra* and *Kadsura* are so similar and exhibit such similar ranges of structural variability that the two genera can be separated at present only upon the basis of differences in their reproductive parts. The Schisandraceae differ, however, from other woody plants of ranalian affinities in the occurrence within them of a peculiar and distinctive type of crystal-bearing sclerenchyma and in peculiarities of structural specialization in the xylem of the stem. How significant are such anatomical differences? Do they preclude relatively close genetic relationship, for example between *Illicium* and the Schisandraceae? It should be emphasized in this connection that differences of comparable magnitude occur not infrequently in families having both arboreal and scandent representatives. In fact, the structural differences in the xylem are no greater than those that differentiate arboreal from scandent species of such genera as *Bauhinia* and *Gnetum*. Therefore, in comparing *Illicium* and the Schisandraceae, it is essential to allow for the acceleration of structural specialization in plants, viz. *Schisandra* and *Kadsura*, that have acquired a climbing habit of growth.

Fortunately, the first-formed secondary xylem of vines and lianas frequently affords valuable clues regarding the general level of structural

specialization in the trees or shrubs from which such scandent plants were derived. Thus, the inner wood in the less modified parts of the stems of *Schisandra* and *Kadsura* clearly indicates that these genera were derived from plants having a typically eustelic structure and a relatively primitive type of secondary xylem in which the multiseriate rays extended outward from the interfascicular parts of the eustele. Although the first-formed secondary xylem in the less modified parts of *Schisandra* and *Kadsura* resembles the later-formed wood of *Illicium*, it is evident that these scandent genera cannot have been derived directly from *Illicium*. This is due to the fact that modification of the eustele and reduction of the multiseriate rays is more advanced in *Illicium* than in the scandent genera.

However, the available anatomical evidence does not negate the derivation of the three genera from a common ancestor. Such a possibility of relatively close genetic relationship between *Illicium* and the Schisandraceae is strengthened by similarities in the cuticles, the stomata, the "ethereal oil" cells and particularly the "mucilage" cells of these plants. "Ethereal oil" cells and stomata, having subsidiary cells oriented parallel to the guard cells, are of common occurrence in various families of the more woody ranalian complex, and taken by themselves are not indicative necessarily of specific, rather than of generalized, ranalian affinities. On the contrary, the peculiar elongated or cambiform "mucilage" cells, which occur so characteristically in the phloem of *Illicium* and the Schisandraceae, have not been encountered by us in other woody representatives of the ranalian complex. Furthermore, the unilacunar nodes of *Illicium*, *Schisandra* and *Kadsura*—in contrast to the prevailingly trilacunar or multilacunar nodes of the Winteraceae, Degeneriaceae, Himantandraceae, Magnoliaceae, Trochodendraceae, etc.—are likewise indicative of possibly close genetic relationship.

Detailed studies of the comparative anatomy of the vegetative organs of woody ranalian families reveal no cogent evidence for including either *Illicium* or the Schisandraceae in the Magnoliaceae. When constituted of the ten genera—*Liriodendron*, *Magnolia*, *Manglietia*, *Michelia*, *Talauma*, *Kmeria*, *Aromadendron*, *Alcimandra*, *Pachylarnax* and *Elmerrillia*—as suggested by Dandy (4), the Magnoliaceae are a very natural grouping of plants which exhibit a relatively high degree of structural uniformity in all of their vegetative and reproductive parts. The inclusion of *Drimys* and its allies, *Illicium*, *Schisandra*, and *Kadsura* introduces structurally incongruous elements which are only remotely related to the Magnoliaceae (*sensu stricto*). Thus, the wide evolutionary gap between the vesselless xylem of the Winteraceae and that of the vessel-bearing Magnoliaceae precludes close relationship between the two groups of plants, as does the unusually high degree of structural specialization and complexity in the nodes and leaves of the Magnoliaceae. Similarly, widely divergent and entirely different trends of structural specialization in the xylem, phloem, nodes and leaves of *Illicium*, *Schisandra*, and *Kadsura* serve as a serious obstacle to the inclusion of these genera in the Magnoliaceae. That such

conclusions are strengthened by detailed investigations of the reproductive parts of these plants will be shown in a subsequent paper. The significance of recent publications of Lemesle and Ozenda will be discussed in this second contribution.

LITERATURE CITED

1. BAILEY, I. W. and CHARLOTTE G. NAST. The comparative morphology of the Winteraceae I. Pollen and stamens. *Jour. Arnold Arb.* 24: 340-346. 1943.
2. BARGHOORN, E. S. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. II. Modification of the multiseriate and uniseriate rays. *Amer. Jour. Bot.* 28: 273-282. 1941.
3. BLENK, P. Ueber die durchsichtigen Punkte in den Blättern. *Flora* 42: 52-55. 1884.
4. DANDY, J. E. The genera of the Magnoliaceae. *Kew Bulletin*. 1927: 257-264. 1927.
5. FLORIN, R. Studien über die Cycadales des Mesozoikums. *Kungl. Svenska Vetensk. Handl.* 12(5): 1-134. 1933.
6. FOSTER, A. S. The foliar sclereids of *Trochodendron aralioides* Sieb. and Zucc. *Jour. Arnold Arb.* 26: 155-162. 1945.
7. HABERLANDT, G. *Physiologische Pflanzenanatomie*. Leipzig. 1904.
8. KRIBS, D. A. Salient trends of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* 96: 547-557. 1935.
9. SMITH, A. C. The families Illiciaceae and Schisandraceae. *Sargentia* 7: 1-224. 1947.
10. SOLEREDER, H. *Systematische Anatomie der Dicotyledonen*. Stuttgart. 1899.

EXPLANATION OF PLATES

PLATE I

FIG. 1. *Illicium anisatum* L. *H. U.* 15749. Transverse section of the unilacunar node. $\times 10$. FIG. 2. *I. anisatum*. *H. U.* 17326. Transverse section of the petiole showing single broad arc of vascular tissues. $\times 18$. FIG. 3. *I. anisatum*. *H. U.* 17326. Transverse section of the leaf, showing broad arc of vascular tissues. $\times 18$. FIG. 4. *Schisandra chinense* (Turcz.) Baill. *H. U.* 17371. Transverse section of the unilacunar node, showing three separate vascular strands at the base of the leaf. $\times 13$. FIG. 5. *S. chinense*. *H. U.* 17370. Transverse section of the petiole showing three separate strands of vascular tissues. $\times 18$. FIG. 6. *S. chinense*. *H. U.* 17370. Transverse section of the leaf showing single arc of vascular tissues. $\times 18$.

PLATE II

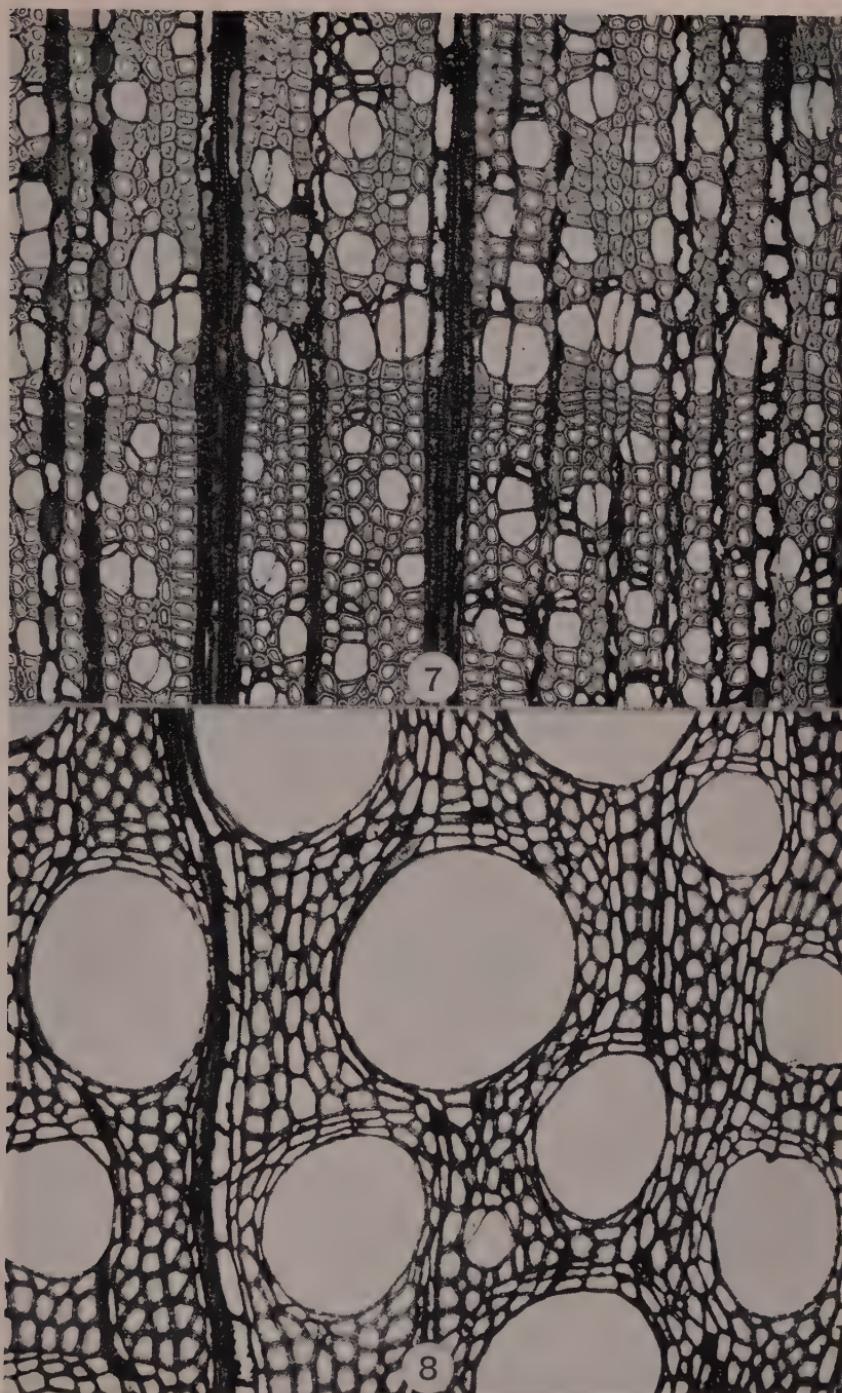
FIG. 7. *Illicium*. *Y. U.* 24057. Transverse section of the wood from the outer part of an old stem, showing heterogeneous rays and distribution of vessels and wood parenchyma. $\times 120$. FIG. 8. *Kadsura scandens* (Bl.) Bl. *H. U.* 17341. Transverse section of the wood, showing huge vessels, large thin-walled tracheids and abaxial paratracheal wood parenchyma. $\times 120$.

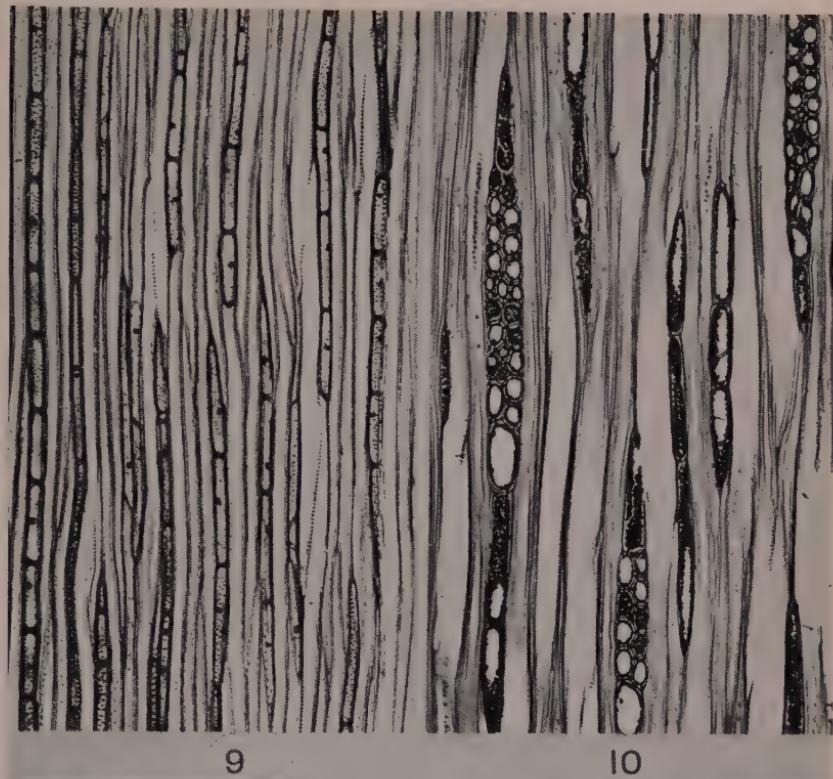
PLATE III

FIG. 9. *Illicium*. *H. U.* 15763. Tangential longitudinal section of wood close to the primary body showing uniseriate rays only. $\times 120$. FIG. 10. *Illicium*. *H. U.* 11175. Tangential longitudinal section of wood from the outer part of an older stem, showing both uniseriate and triseriate rays. $\times 120$. FIG. 11. *I. Masa-Ogatai* (Makino) A. C. Smith. *Kanehira* 3386. Lower surface of the leaf showing stomata, secretory cell, ribbed cuticle and undulating contour of epidermal cells. $\times 250$.



MORPHOLOGY OF *ILlicium*, *SCHISANDRA* AND *KADSURA*



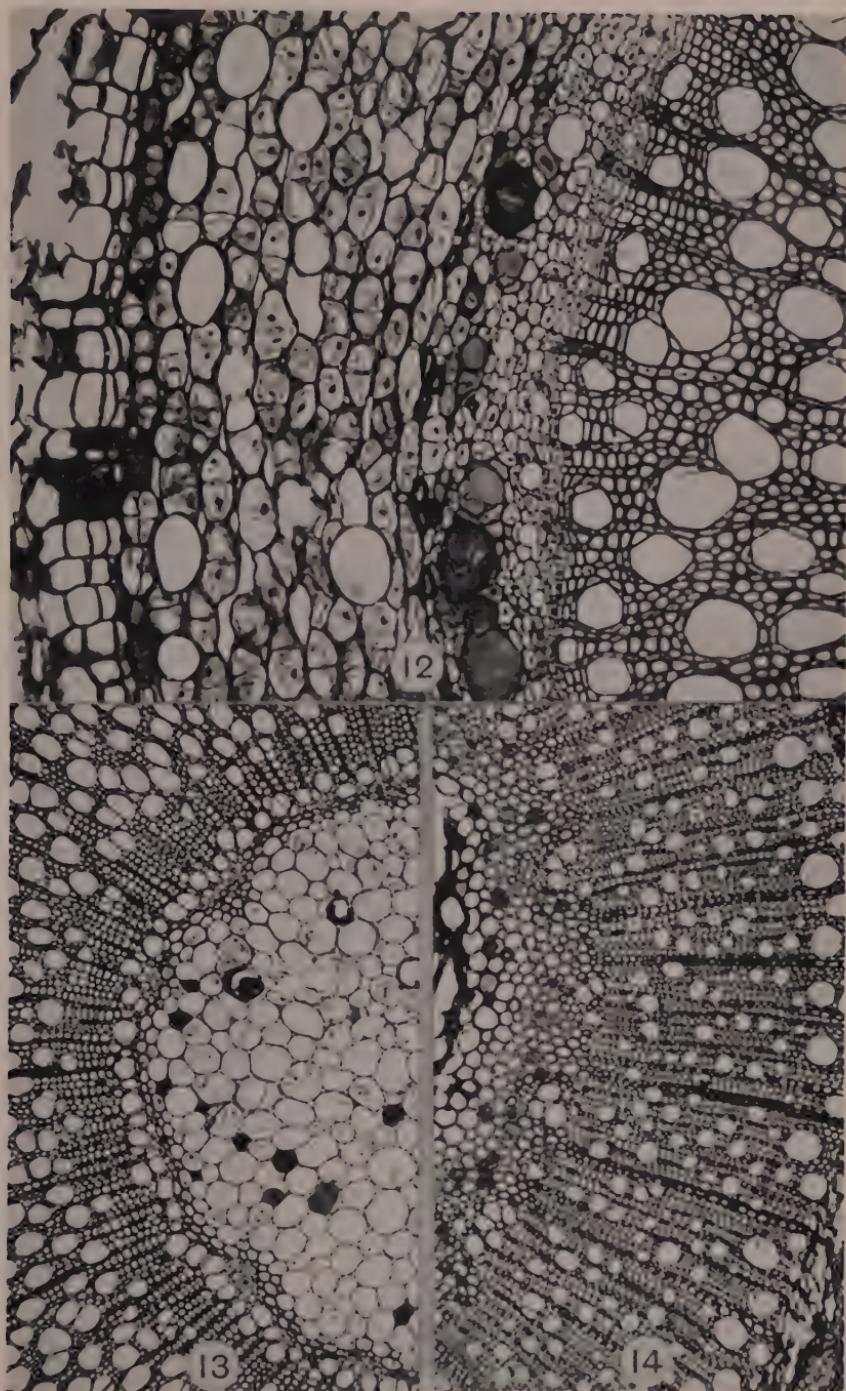


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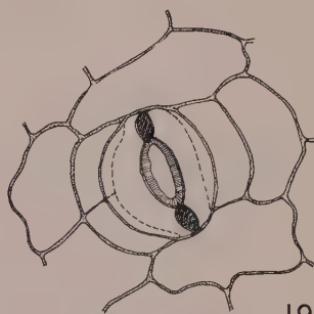
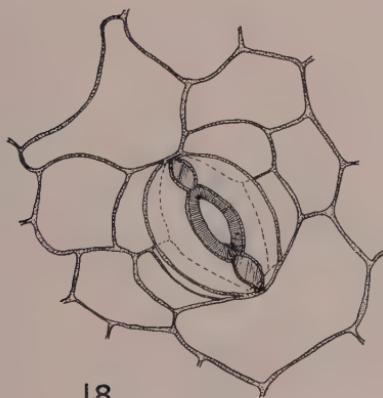
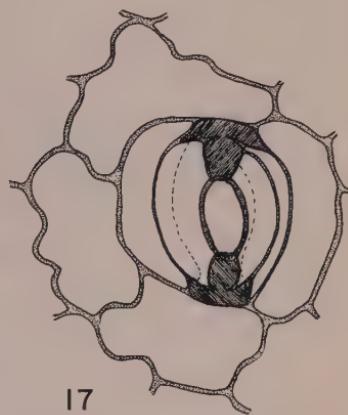
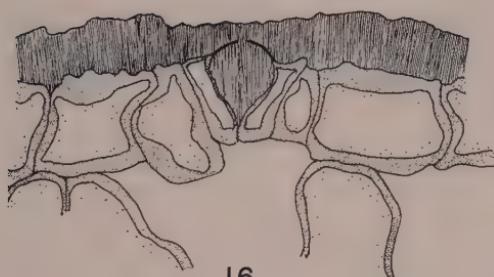
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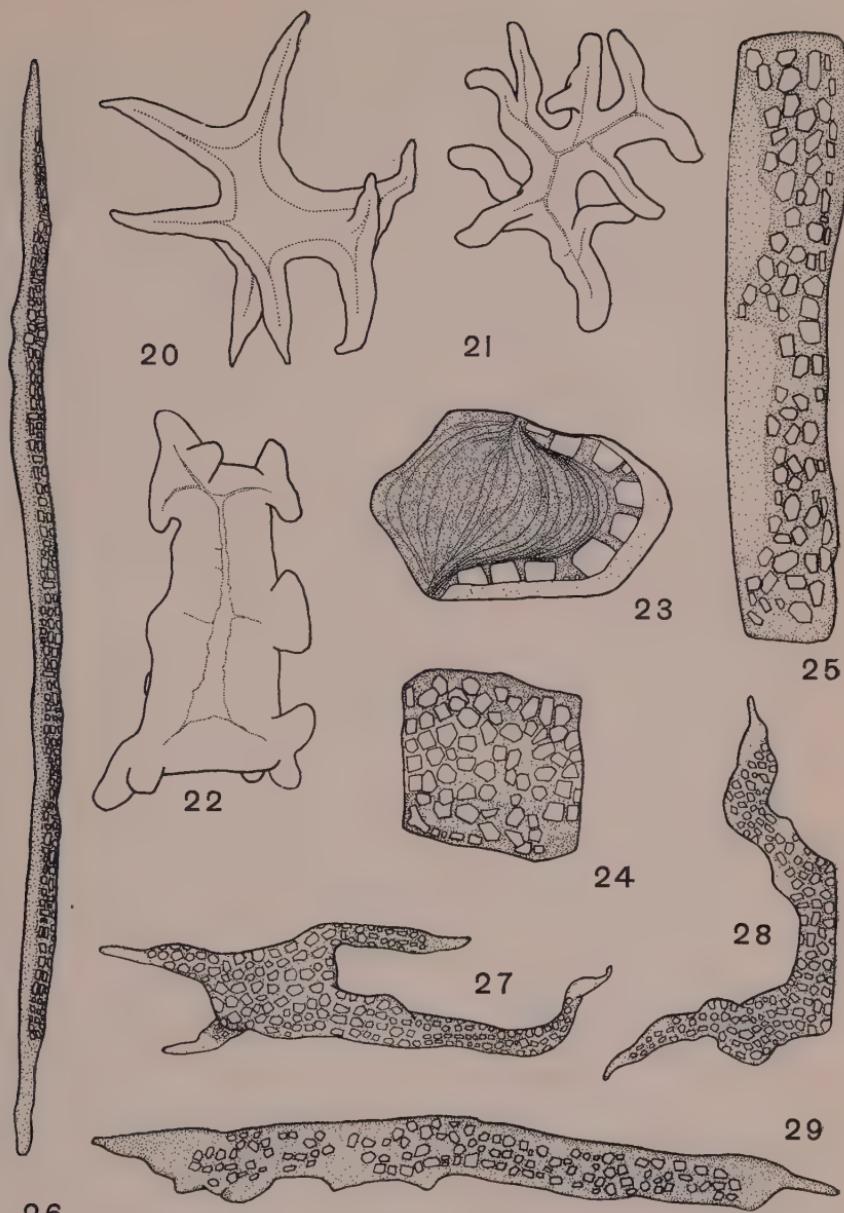


MORPHOLOGY OF *ILlicium*, *SCHISANDRA* AND *KADSURA*



MORPHOLOGY OF *ILlicium*, *SCHISANDRA* AND *KADSURA*





MORPHOLOGY OF *ILlicium*, *SCHISANDRA* AND *KADSURA*

PLATE IV

FIG. 12. *Schisandra chinense* (Turcz.) Baill. *H. U.* 17370. Transverse section of the outer part of a young stem, showing "mucilage cells" with darkly stained contents in outer phloem and large oval "resin cells" in the cortex. $\times 120$. FIG. 13. *The same*. Central part of the stem, showing continuous ring of metaxylem vessels succeeded by a narrow zone of vesselless wood. $\times 50$. FIG. 14. *Kadsura coccinea* (Lem.) A. C. Sm. *Tso* 20393. Transverse section of part of a young stem, showing discrete strands of primary xylem with multiseriate rays extending outward from the parenchymatous interfascicular lacunae. $\times 50$.

PLATE V

FIG. 15. *Illicium philippinense* Merr. *Wilson* 10182. Transverse section through center of a stomatal apparatus. $\times 760$. FIG. 16. *The same*. Transverse section of the stomatal apparatus cut through the cuticular intrusion. $\times 760$. FIG. 17. *The same*. Surface view of a stomatal apparatus. $\times 470$. FIG. 18. *Kadsura coccinea* (Lem.) A. C. Sm. *Tso* 20740. Surface view of stomatal apparatus. $\times 300$. FIG. 19. *The same*. Surface view of stomatal apparatus. $\times 300$.

PLATE VI

FIG. 20. *Illicium leiophyllum*. A. C. Sm. *W. J. Tutterer* (Hongk. Herb.) 6 (TYPE). A foliar sclereid with large lumen and tapered branches. $\times 250$. FIG. 21. *I. Simonsii* Maxim. *Ten* 160. A foliar sclereid with occluded lumen and blunt branches. $\times 250$. FIG. 22. *I. Staphfi* Merr. *J. & M. S. Clemens* 35060. A massive rectangular sclereid. $\times 250$. FIG. 23. *Schisandra elongata* (Bl.) Baill. *H. U.* 15775. Crystal-bearing sclerenchymatous cell in sectional view. $\times 640$. FIG. 24. *Schisandra plena* A. C. Sm. *Henry* 10854 (TYPE). Crystal-bearing sclerenchymatous element. $\times 300$. FIG. 25. *The same*. Crystal-bearing sclerenchymatous element. $\times 300$. FIG. 26. *Schisandra propinqua* (Wall.) Baill. var. *intermedia* A. C. Sm. *Hooker & Thomson* s.n. Crystal-bearing sclerenchymatous element. $\times 210$. FIG. 27. *Kadsura borneensis* A. C. Sm. *J. & M. S. Clemens* 31889. Crystal-bearing sclerenchymatous element. $\times 210$. FIG. 28. *The same*. Crystal-bearing sclerenchymatous element. $\times 210$. FIG. 29. *Schisandra propinqua* (Wall.) Baill. var. *intermedia* A. C. Sm. Crystal-bearing sclerenchymatous element. $\times 300$.

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IN GENERAL PLANT MORPHOLOGY
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THE CYPERACEAE COLLECTED IN NEW GUINEA BY
L. J. BRASS, III*

S. T. BLAKE

With one text-figure

THIS PAPER deals exclusively with the genera of the Rhynchosporoideae. A monograph of this tribe was commenced by G. Kükenthal prior to, and was continued during the war, but it was only after this paper had been almost completed that most of his published work became available. For the most part my treatment agreed well with that of Kükenthal; when it was found to differ, the group concerned was re-examined, but occasionally it was found not possible to reconcile the two points of view. These differences of opinion are discussed under the species concerned.

Schoenus Linnaeus

Schoenus falcatus R.Br. Prodr. 232. 1810; Kükenth. in Engl. Bot. Jahrb. 69: 259. 1938, in Fedde, Repert. 44: 24. 1938, 48: 247. 1940, in Bull. Jard. Bot. Buitenz. III, 16: 304. 1940.

PAPUA: Western Division: Penzara, between Morehead and Wassi Kussa Rivers, *Brass 8469*, Dec. 1936, savannah-forest. Central Division: Hisiu, *Carr 11448*, Feb. 1935; sea-level, open savannah land (about 42 in. tall).

SOLOMON ISLANDS: Olevuga Island: N'Gela, *Brass 3485*, Jan. 1933, stiff sedge on grasslands.

New for the Solomon Islands. Known previously from northern Australia, New Guinea and other parts of Malaysia, and Tonkin.

Schoenus punctatus R.Br. Prodr. 232. 1810; Kükenth. in Fedde, Repert. 48: 247. 1940.

PAPUA: Western Division: Tarara, Wassi Kussa R., *Brass 8388*, Dec. 1936, savannah-forest, characteristic cover on gray soil flats.

Brass's collection was cited by Kükenthal, l.c. The species is elsewhere known from northern Australia, Marianne Islands and Siam.

Schoenus sparteus R.Br. Prodr. 231. 1810; Kükenth. in Fedde, Repert. 44: 28. 1938, 48: 247. 1940.

PAPUA: Western Division: Tarara, Wassi Kussa R., *Brass 8534*, Dec. 1936, in poorly drained savannah forest; Tarara, Wassi Kussa R., *Brass 8578*, Dec. 1936, savannah forest, very abundant on wet flats; Tarara, Wassi Kussa R., *Brass 8726*, Jan. 1937, open savannah-forest, covering poorly drained flats (young growths after burning); Mai Kussa R., *W. MacGregor* in 1890 (herb. Melbourne).

Brass's three collections were cited by Kükenthal, 1940, l.c. The species appears to be confined to northern and north-eastern Australia and New Guinea.

* Botanical Results of the Richard Archbold Expeditions. See Jour. Arnold Arb. 28: 207-229. 1947.

Schoenus laevinux (Kükenth.) Ohwi in *Jour. Japan. Bot.* 18: 136. 1942, in *Bot. Mag. Tokyo* 56: 206. 1942.

Schoenus melanostachyus R.Br. var. *laevinux* Kükenth. in *Engl. Bot. Jahrb.* 59: 52. 1924.

Schoenus tendo (Hook.f.) Hook.f. var. *laevinux* (Kükenth.) Kükenth. in *Fedde, Repert.* 44: 30. 1938, in *Engl. Bot. Jahrb.* 69: 259. 1938, in *Fedde, Repert.* 48: 247. 1940.

NETHERLANDS NEW GUINEA: Hollandia and vicinity, *Brass 8905*, June-July, 1938, alt. 30 m., several clumps on a cliff face in rain-forest (stems pendent); 18 km. SW. of Bernhard Camp, Idenburg R., *Brass 12474*, Feb. 1939, alt. 2150 m., associated with ferns and *Lycopodium* on open rock slide.

The species is apparently confined to New Guinea, although externally it is very similar to *S. tendo* var. *triander* Kükenth. from New Caledonia, of which I have seen flowering material only. It resembles *S. melanostachyus* in habit, but has a smooth (not rugose) glassy, white (not ferruginous), obovoid rather than ovoid nut, and it differs from *S. tendo* in the symmetrical glassy nut, absence of hypogynous bristles, non-sulcate culms and more copious panicles.

Schoenus calostachyus (R.Br.) Poir. *Encycl. Suppl.* 2: 251. 1811; F.Muell. *Pap. Pl.* 2: 69. 1890; Valck. *Suring.* in *Nova Guin. Bot.* 8: 707. 1912; Kükenth. in *Fedde, Repert.* 44: 73. 1938, 48: 248. 1940; Ohwi in *Bot. Mag. Tokyo* 56: 207. 1942.

Chaetospora calostachya R.Br. *Prodr.* 233. 1810.

Cyclocampe waigiovensis Steud. *Synops. Cyper.* 156. 1855.

PAPUA: Western Division: Dagwa, Oriomo R., *Brass 5912*, Feb.-March 1934, alt. 40 m., common on rather damp open grass slopes; Tarara, Wassi Kussa R., *Brass 8564*, Dec. 1936, savannah-forests, common on gray soils; Tarara, Wassi Kussa R., *Brass 8535*, Dec. 1936, poorly drained savannah-forests; Mai Kussa R., *W. MacGregor* in 1890 (herb. Melbourne).

Brass's collections were cited by Kükenthal, 1940 l.c. The species extends from New South Wales to Malaya.

Schoenus curvulus F.Muell. in *Trans. Roy. Soc. Vict. n.s.* 1(2): 36. 1889; C. B. Clarke in *Kew Bull.* 1899: 114. 1899; Valck. *Suring.* in *Nova Guin. Bot.* 8: 707. 1912; Kükenth. in *Fedde, Repert.* 44: 76. 1938, in *Engl. Bot. Jahrb.* 69: 260. 1938, in *Fedde, Repert.* 48: 248. 1940, in *Bull. Jard. Bot. Buitenz.* III, 16: 305. 1940.

NETHERLANDS NEW GUINEA: Mt. Wilhelmina, 7 km. NE. of top, *Brass & Meyer-Drees 9973*, Sept. 1938, alt. 3560 m., common on wet grass slopes.

PAPUA: Central Division: Mt. Albert Edward, *Brass 4447*, May-July 1933, alt. 3680 m., massed under rocks on marshy bank of a grassland stream; Mt. Tafa, *Brass 5006*, May-Sept. 1933, alt. 2400 m., in small erect tufts on dry crumbling soil of an exposed ridge point; Murray Pass, Wharton Range, *Brass 4672*, June-Sept. 1933, alt. 2840 m., common on open grasslands, most frequently found under shelter of tree-ferns; Mt. Victoria, *W. MacGregor* in 1889 (herb. Melbourne); near summit of Owen Stanley Ranges, *W. MacGregor* in 1889 (type in herb. Melbourne, Brisbane); without definite locality, *W. MacGregor* in 1894 (herb. Melbourne, Brisbane).

Confined to New Guinea. *Brass 4447* was cited by Kükenthal in *Fedde, Repert.* 48: 248. 1940.

In his original description, F. Mueller lays considerable stress on the curved or twisted stems and leaves, but the appearance of the specimens suggest that the twisting is due to the method of collecting or their preparation. In common with other specimens collected by MacGregor

(cited in this and earlier papers) they give the impression of having been hastily pulled and crammed into a pocket.

The species was described by Kükenthal in his revision of the genus in Fedde, Repert. 44: 76. 1938 as having 1-2-noded culms, leaves with circinate tips and spikelets 6-8 mm. long. The leaves of the type-collection as well as of Brass's specimens have straight tips, the spikelets are 6-7 mm. long or sometimes as short as 5 mm. on Brass's specimens. Owing to the unusually long leaf-sheaths, the number of nodes is not always easy to ascertain without stripping off the leaves, but certainly sometimes reaches 4. Sometimes the whole of the culm beneath the inflorescence is concealed by the sheaths.

Schoenus curvulus is rather closely allied to some forms of *S. apogon* R. & S., differing chiefly in the looser inflorescence with fewer larger spikelets, longer and relatively narrower elliptic-oblong nuts more prominently apiculate and nearly smooth, and in the hypogynous bristles longer than the nut. *Schoenus erythrosiphon* Ohwi in Bot. Mag. Tokyo 56: 205. 1942, appears to be very similar from the description, differing chiefly in the smaller spikelets 4-5 mm. long, and shorter anthers with the connective only shortly produced.

Schoenus setiformis sp. nov. (sect. *Helothrix* (Nees) Kükenth.). FIG. 1.

Herba perennis, rhizomate abbreviato. Culmi plurimi, dense caespitosi, simplices, tenuiter setacei, rigidi, circiter 5-25 cm. alti, 0.25-0.4 mm. crassi, teretes, striati ceterum laeves, glabri, sub inflorescentia 1-2-nodes vel enodes, foliati. Folia basilaria et caulina setacea, culmo breviora, circiter 0.25-0.4 mm. lata, supra canaliculata, subtus convexa leviter striata, apicem versus scaberula; vaginæ 1-2 cm. longae, purpureae, ore truncato imberbes, basilaribus apertæ, caulinae clausæ. Panicula plerumque capitata, 7-12 mm. longa lataque, 7-12-spiculata, e fasciculis 2 valde approximatis composita, interdum fasciculo tertio distante addito; rami in quoque fasciculo 1-7, indivisi, usque ad 6 mm. longi. Bracteæ foliaceæ inflorescentiam superantes vel inferiores longe superantes, ore vaginæ imberbes. Spiculae breviter pedicellatae, nigricantes vel purpureo-tinctæ, lanceolatae vel oblongo-lanceolatae, 3.3-4.5 mm. longæ, 0.9-1.2 mm. latae, 1-3-floræ. Glumæ 6-7 nigricantes vel atropurpureæ, nitidulæ, lanceolatae, carina concolore sursum scaberula percursæ, marginibus angustissime albo-hyalinis glabrae, inferiores 3-4 vacuae latiores acutiores, superiores anguste obtusæ 2.5-3.3 mm. longæ. Setae hypogynæ 6, ± ferrugineæ vel purpurascentes, antrorsim scabrae, nucem superantes. Stamina 3, antheræ lineares flavae, connectivum mediocriter (circiter 0.2-0.3 mm.) productum subulatum, circiter 1.3-1.4 mm. longæ. Stylus brunneus, 1 mm. longus; stigmata 3, stylo aequilonga. Nux ellipsoidea vel angustius ovoidea, apice vel utrinque acuta, apiculata, prominule tricostulata, lateribus convexa, pallida mox brunnescens, nitida, fere omnino laevis cellulis extimis minimis valde obscuris, 1.1-1.3 mm. longa, 0.5-0.65 mm. lata.

NETHERLANDS NEW GUINEA: Mt. Wilhelmina, 11 km. NE. of top, *Brass & Meyer-Drees* 9724, Sept. 1938, alt. 3400 m., wet grassy western slope; Mt. Wilhelmina, 7 km. NE. of top, *Brass & Meyer-Drees* 9998, Sept. 1938, alt. 3560 m., gray clay of old landslips, plentiful; Lake Habbema, *Brass* 9478, Aug. 1938, alt. 3225 m.,

niches on a precipitous rock face; 9 km. NE. of Lake Habbema, Brass 10561, Oct. 1938, alt. 2750 m., few clumps in open stony bed of stream; 9 km. NE. of Lake Habbema, Brass 10923 (TYPE), Oct. 1938, alt. 2800 m., common on landslip with *Imperata cylindrica*.

This species is distinguished particularly by the very slender but rigid culms and leaves, the few-spikeleted inflorescence which is usually reduced to two approximated fascicles of about 8–10 spikelets in all (though occasionally there is a third fascicle of 1–3 spikelets lower down), and the shining smooth nut with tiny indistinct external cells, stramineous when young but soon becoming brown and overtopped by the more or less ferruginous or purple hypogynous bristles. It comes under series *Microcarpae* Benth. or sect. *Helothrix* (Nees) Kükenth., and is allied to *S. curvulus* F. Muell., *S. erythrosiphon* Ohwi and *S. apogon* R. & S., but differs from all three in the extremely slender though rigid and straight culms and leaves, coloured hypogynous bristles, and quite smooth more or less brown (not white) nut with very small and obscure external cells. From the first two it differs also in the short leaf-sheaths, scanty capitate inflorescence of few shortly pedicellate mostly smaller spikelets and smaller style, and from *S. curvulus* in the shorter anthers with shorter appendage. From *S. apogon* it also differs in the narrower acute nut overtopped by the bristles, and, except, for reduced states, in the small capitate inflorescence.

Perhaps the plants referred to *S. apogon* by Ridley in Trans. Linn. Soc. II, Bot. 9: 243. 1916, belong here.

Schoenus foliatus (Hook.f.) S. T. Blake in Proc. Roy. Soc. Queensl. 51: 48. Feb., 1940.

Schoenus foliatus (Hook.f.) Kükenth. in Fedde, Repert. 48: 248. Sept. 1940.

Schoenus axillaris (R.Br.) Poir. Encycl. Suppl. 2: 251. 1811, non Lam.

Schoenus subaxillaris Kükenth. in Fedde, Repert. 44: 89. 1938, in Engl. Bot. Jahrb. 69: 260. 1938.

Chaetospora axillaris R.Br. Prodr. 233. 1810.

Helothrix pusilla Nees in Ann. Nat. Hist. sér. I, 6: 45. 1841, non *Schoenus pusillus* Sw.

Scirpus foliatus Hook.f. in London Jour. Bot. 3: 414. 1844.

Helothrix axillaris (R.Br.) Palla in All. Bot. Zeitschr. 8: 68. 1902.

NETHERLANDS NEW GUINEA: Lake Habbema, Brass 9236, Aug. 1938, alt. 3225 m., growing with mosses on sunny seepages.

New for Netherlands New Guinea; previously recorded from North-East New Guinea, the more southern parts of Australia, New Zealand and the Chatham Islands.

The combination *Schoenus foliatus* was published independently by Dr. Kükenthal and myself. My paper has priority by slightly over seven months.

Carpha R. Brown

Carpha alpina R.Br. Prodr. 230. 1810; F.Muell. in Trans. Roy. Soc. Vict. n.s. 1(2): 35. 1889; C. B. Clarke in Kew Bull. 1899: 114. 1899; Valck. Suring. in Nova Guin. Bot. 8: 706. 1912; H. Pfeiff. in Fedde, Repert. 29: 178. 1931; Kükenth. in Fedde, Repert. 47: 112. 1939.

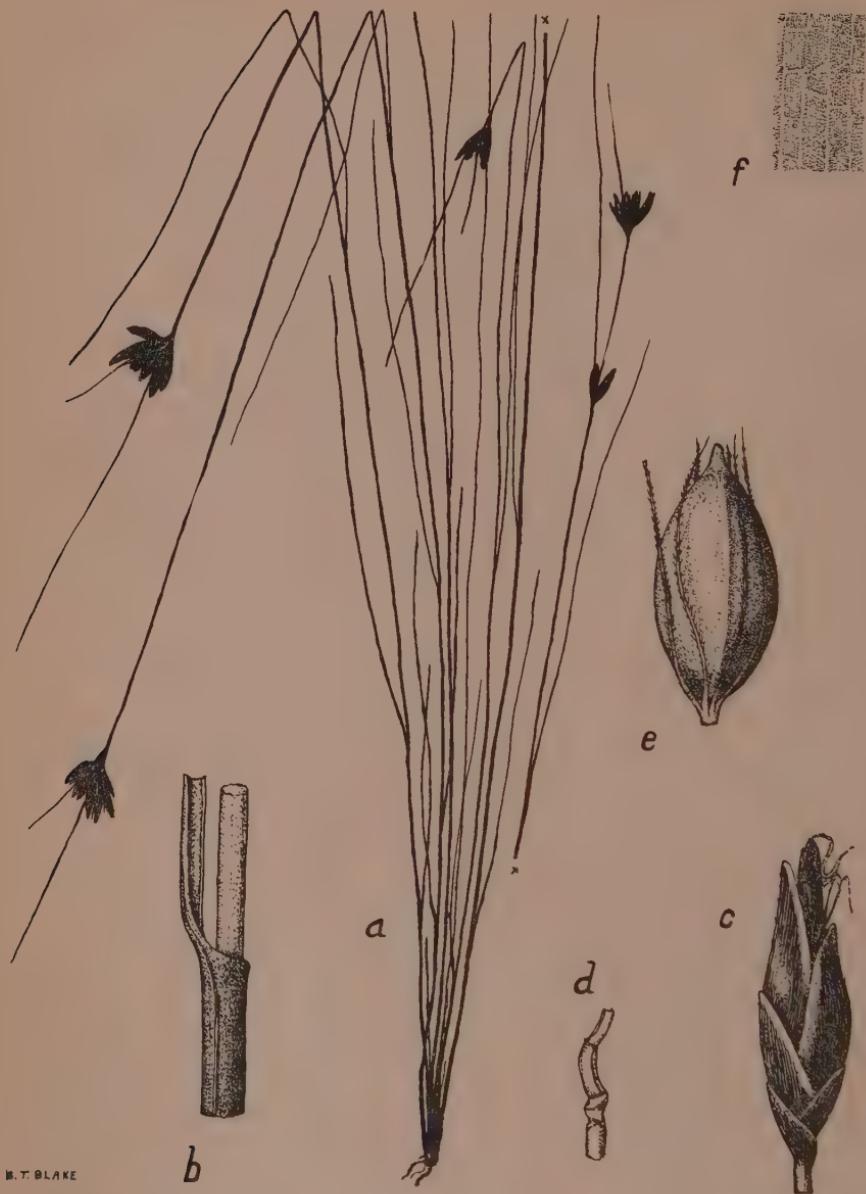


FIG. 1. *Schoenus setiformis* S. T. Blake: a. portion of plant, $\times 1$; b. portion of culm with apex of cauline leaf-sheath and base of blade, $\times 10$; c. spikelet, $\times 10$; d. rhachilla of spikelet, glumes and flowers removed, $\times 10$; e. nut, with torus and hypogynous bristles, but with filaments removed, $\times 30$; f. surface of nut, $\times 100$. From type-specimen.

NETHERLANDS NEW GUINEA: Northern slopes of Mt. Wilhelmina, *Brass & Meyer-Drees 10078*, Sept. 1938, alt. 4160 m., alpine grassland, covering sandy banks of a small stream; Mt. Wilhelmina, 7 km. NE. of top, *Brass & Meyer-Drees 9925*, Sept. 1938, alt. 3650 m., alpine grassland, very abundant in marshy hollows (clumps 20-30 cm. high).

PAPUA: Central Division: Mt. Albert Edward, *Brass 4299*, May-July 1933, alt. 3800 m., very plentiful on alpine seepage slopes (leaves somewhat glaucous); near summit of Owen Stanley Range, *W. MacGregor* in 1889 (herb. Brisbane, Melbourne); Mt. Knutsford, *W. MacGregor* in 1889 (herb. Melbourne).

Not previously reported from Netherlands New Guinea. The species occurs in south-eastern Australia, Tasmania and New Zealand.

Carpha schoenoides Banks & Sol. ex Hook.f. Fl. Antarct. 2: 362, t. 148. 1847, from Tierra del Fuego is evidently very closely allied, but appears to differ in the fewer solitary spikelets each 2-flowered with the hypogynous bristles plumose to the tips and a serrate-scabrous style-base.

Costularia C. B. Clarke

Costularia Urvilleana (Gaud.) Kükenth. in Fedde, Repert. 46: 28. 1939.

Carpha arundinacea Brongn. in Duperr. Voy. Coquille Bot. 2: 169, t. 30. 1829, non (Vahl) Boeck.

Carpha Urvilleana Gaud. ex Nees in Linnaea 10: 300. 1834.

Lophoschoenus Urvilleanus (Gaud.) Stapf in Jour. Linn. Soc. Bot. 42: 180. 1914.

NETHERLANDS NEW GUINEA: Hollandia and vicinity, *Brass 8802*, June-July 1938, alt. 5-30 m., plentiful in rather distant clumps on stony patches of dry open slopes.

New for New Guinea. Previously known from Borneo and the Moluccas.

Oreobolus R. Brown

Oreobolus pumilio R.Br. Prodr. 236. 1810; Kükenth. in Engl. Bot. Jahrb. 70: 464. 1940.

Oreobolus Clemensiae Kükenth. in Fedde, Repert. 48: 69. 1940.

NETHERLANDS NEW GUINEA: Lake Habbema, *Brass 9244*, Aug. 1938, alt. 3225 m., one of the characteristic plants of alpine bog turf, carpet forming or in small rounded clumps.

New for Netherlands New Guinea. Kükenthal in Engl. Bot. Jahrb., l.c., records it for North-East New Guinea, but in the same year based his *O. Clemensiae* Kükenth., l.c., on the same collection (which I have not seen), without any reference to his other paper. *Brass 9244* agrees well with the description of *O. Clemensiae* and, except for the somewhat longer leaves, with Tasmanian specimens of *O. pumilio* R.Br. The breadth of the perianth-segments (hypogynous scales) and the colour of the leaf-sheaths and glumes are variable on the Tasmanian plants, and the spikelets of the New Guinea plants are not shorter. It seems likely that Kükenthal has drawn up his description of *O. pumilio* for his revision in Fedde, Repert., l.c., from plants other than Tasmanian. The species, so far as I have seen specimens, is elsewhere known with certainty only from Tasmania and Victoria. The range "Nordaustralien" given by Kükenthal in Engl. Bot. Jahrb., l.c., was due probably to a slip of the pen. The species

has been stated to occur in New Zealand (cf. Kükenthal in Fedde, *Repert.* 48: 67. 1940), but all the specimens I have seen from that region belong to other species.

Oreobolus ambiguus Kükenth. & van Steenis in *Bull. Jard. Bot. Buitenz.* III, 14: 47, fig. 1. 1936; Kükenth. in *Engl. Bot. Jahrb.* 70: 463. 1940, in Fedde, *Repert.* 48: 72. 1940.

NETHERLANDS NEW GUINEA: Lake Habbema, *Brass* 9579, Aug. 1938, alt. 3225 m., one of the characteristic plants of alpine bog turf, carpet forming or in small rounded clumps.

PAPUA: Central Division: Mt. Albert Edward, *Brass* 4470, May-July 1933, alt. 3680 m., common in close masses on alpine seepage slopes.

New for both Netherlands New Guinea and Papua. Previously reported from British North Borneo and North-East New Guinea. The specimens agree well with the original description and figure, except that in *Brass* 9579 the inflorescence consists of a single spikelet.

Cladium P. Browne

Cladium Meyenii (Kunth) Drake, *Ill. Fl. Insul. Maris Pacifici* 335. 1892.

Baumea Meyenii Kunth, *Enum. Pl.* 2: 314. 1837.

Baumea mariscoides Gaud. in *Freycin. Voy. Bot.* 417. 1826.

Cladium mariscoides (Gaud.) F. Villar in *Blanco, Fl. Philipp.* ed 3, *Nov. App.* 309. 1882, non Torr.

Cladium Gaudichaudii W.F.Wight in *Contrib. U.S. Nat. Herb.* 9: 230. 1905; Ohwi in *Bot. Mag. Tokyo* 56: 208. 1942.

Cladium Meyenii (Kunth) Drake var. *Gaudichaudii* (W. F. Wight) Kükenth. in *Engl. Bot. Jahrb.* 69: 260. 1938, in Fedde, *Repert.* 51: 157. 1942.

SOLOMON ISLANDS: Ysabel: Cape Prieto, *Brass* 3478, Jan. 1933, alt. 200 m., common tussock sedge on dry open hillsides; Cape Prieto, *Brass* 3477, Jan. 1933, alt. 200 m., common ground plant on dry open slopes, small tussocks or clumps on loose soil (leaves and stems of bluish appearance). San Cristobal: Hinuahaoro, *Brass* 3021, alt. 900 m., common on old village site (thick clumps, leaves rather glaucous).

New for the Solomon Islands; previously known from the Hawaiian Islands, Marianne Islands, and North-East New Guinea. The specimens cited above form an interesting series, and it is from their study that I have proposed treating *C. Gaudichaudii* as synonymous with *C. Meyenii*. *Brass* 3021 (in flower) and *Brass* 3478 (in nearly mature fruit) are good matches for Hawaiian material (*C. Meyenii*). *Brass* 3477 has less effuse panicles, with the spikelets more numerous in the fascicles and one piece agrees particularly well with Boeckeler's elaborate description of the type or an isotype of *Baumea mariscoides*.

Drake del Castillo, l.c., cites Bentham & Hooker, *Gen. Pl.* 3: 1065. 1883, as the authors of *Cladium Meyenii*, but these authors made no such combination, and merely treat *Baumea* as a section of *Cladium*. The name is not listed in *Index Kewensis*.

Cladium colpodes Lauterb. in Schum. & Lauterb. *Nachtr. Fl. Deutsch. Schutzgeb. Südsee* 59. 1905; Valck. *Suring. in Nova Guin. Bot.* 8: 707. 1912; Kükenth. in *Engl. Bot. Jahrb.* 59: 52. 1924, 69: 260. 1938, in Fedde, *Repert.* 51: 155. 1942; Kanehira in *Jour. Dept. Agr. Kyushu Univ.* 4: 276. 1935.

Cladium globiceps C. B. Clarke in Kew Bull. Add. Ser. 8: 46. 1908.
Cladium juncoides Elmer in Leafl. Philipp. Bot. 3: 854. 1910.
Cladium sinuatum Ridl. in Trans. Linn. Soc. II, Bot. 9: 243. 1916.
Cladium glomeratum (Gaud.) H. Pfeiff. in Fedde, Repert. 23: 349. 1927, non R.Br.
Cladium globiceps C. B. Clarke var. *colpodes* (Lauterb.) Kükenth. in Bull. Jard. Bot. Buitenz. III, 16: 310. 1940.
Cladium Meyenii (Kunth) Drake var. *juncoides* (Elmer) Kükenth. in Bull. Jard. Bot. Buitenz. III, 16: 310. 1940,* in Fedde, Repert. 51: 157. 1942.
Baumea glomerata Gaud. in Freycin. Voy. 46, t. 29. 1826.
Mariscus colpodes (Lauterb.) Fernald in Rhodora 25: 53. 1923.
Mariscus globiceps (C. B. Clarke) Fernald, l.c.

NETHERLANDS NEW GUINEA: Hollandia and vicinity, Brass 8803, June-July 1938, alt. 20 m., plentiful in dense somewhat glaucous clumps on partly bare ground of dry deforested slopes.

The species was originally described as *Baumea glomerata* by Gaudichaud, but on its transfer to *Cladium* the epithet *glomeratum* was unavailable owing to the existence of *Cladium glomeratum* R.Br. Prodr. 237. 1810, quite a different plant. C. B. Clarke, l.c., accordingly proposed for it a new name, *Cladium globiceps*. Pfeiffer, however, ignored Brown's earlier homonym, and wrongly took up Gaudichaud's epithet. Both Clarke and Pfeiffer treated *C. globiceps* and *C. colpodes* as distinct species. Kükenthal at first (1924, l.c.) regarded them as conspecific, though later (1938, l.c.) he treated them as varietally distinct. However, in so doing, he erred in not taking up the earlier name *C. colpodes* for the species. Still later (1942, ll.cc.), he treated them as specifically distinct. I have been unable to find any characters to distinguish *C. globiceps*, *C. juncoides* or *C. sinuatum* from *C. colpodes*, and so propose to treat the first three as synonyms of the last-mentioned. *Cladium Meyenii* (Kunth) Drake, of which Kükenthal treats *C. juncoides* as a variety, appears to me to differ by reason of its wider leaves and slightly larger spikelets with larger reddish nuts. In this extended sense *C. colpodes* is fairly widely spread in Malaysia.

Cladium brevipaniculatum (Kükenth.) Kükenth. in Fedde, Repert. 51: 176. 1942.
Cladium Gunnii Hook.f. var. *brevipaniculatum* Kükenth. in Engl. Bot. Jahrb. 69: 260. 1938.

PAPUA: Central Division: Murray Pass, Wharton Range, Brass 4644, June-Sept. 1933, alt. 2840 m., growing thickly in a swampy hollow on grassland.

New for Papua; previously known only from North-East New Guinea. The specimen is very young, but appears to belong here. This collection was cited under *Lepidosperma chinense* Nees & Meyen by Kükenthal in Fedde, Repert. 50: 124. 1941, but the absence of hypogynous bristles does not accord with the characters of this genus, and the general facies of the plant is that of *Cladium*.

?*Cladium glomeratum* R.Br. Prodr. 237. 1810.

NETHERLANDS NEW GUINEA: Lake Habbema, Brass 9443, Aug. 1938, alt. 3225 m., forming very open tufted stands 1.2-1.5 m. high in sandy marginal shallows and on marshy shores of lake.

* Kükenthal cites *Cladium Meyenii* (Künth.) Benth. et Hook.; see discussion under previous species.

The material is sterile, but appears to belong to this species which is widely spread in Australia, New Zealand and New Caledonia, extending to SE. Asia. In Fedde, Repert. 51: 171. 1942, Kükenthal records it for North-East New Guinea under the name *Cladium rubiginosum* (Soland.) Domin, a name which I have shown to be invalid in Trans. Roy. Soc. S. Austr. 67: 58. 1943, because the basonym *Schoenus rubiginosus* Soland. ex Forst. Prodr. 89. 1786 is a *nomen nudum*.

Cladium undulatum Thw. Enum. Pl. Zeyl. 353. 1864; Kükenth. in Fedde, Repert. 51: 162. 1942.

Cladium undulatum Thw. var. *fimbristyloides* (F. Muell.) Domin in Biblioth. Bot. 20(85): 473. 1915.

Lepidosperma Zeylanicum Lindl. ex Boeck. in Linnaea 38: 332. 1874.

Carpha junciformis Boeck. in Linnaea 38: 267. 1874.

Chaetospora fimbristyloides F. Muell. Fragm. Phyt. Austr. 9: 34. 1875.

Tricostularia fimbristyloides (F. Muell.) Benth. Fl. Austral. 7: 384. 1878.

Schoenus fimbristyloides (F. Muell.) F. Muell. First Census Austral. Pl. 128. 1882.

PAPUA: Western Division: Tarara, Wassi Kussa R., Brass 8410, Dec. 1936, savannah-forest, abundant on sour gray soil.

Brass's collection, the only one known from New Guinea, was cited by Kükenthal, l.c. The species ranges from northern Australia to Malaya and Ceylon, and, as indicated in the synonymy above, has been assigned to various genera. From *Chaetospora* (*Schoenus*) and *Carpha* it differs in the more or less spirally arranged glumes and in habit; from the former also in the short internodes of the rhachilla of the spikelet and the nut with its persistent style-base, and from the latter in the broad small nut with short style-base and short not plumose hypogynous bristles. From *Lepidosperma* it differs in foliage and somewhat in inflorescence, in the unthickened hypogynous bristles, and in that it is the lower flower (when more than one is present) which is fertile; the texture of the exocarp of the nut is also different. From *Tricostularia* it differs in foliage and inflorescence, in that it is the lower flower which is fertile, and in the persistent style-base. It differs also from the majority of species usually referred to *Cladium* in habit and in the thin marcescent exocarp of the nut. For the present I have accepted the arrangement of this species proposed by C. B. Clarke in Hook.f. Fl. Brit. Ind. 7: 674. 1894, and followed by Kükenthal, l.c., chiefly because I have seen no specimens from beyond Australia and New Guinea. Kükenthal's description of the leaves of *Cladium undulatum* does not apply to our plant, in which they are spirally arranged and flattened or with involute margins, not distichous and semiterete.

Gahnia J. R. & G. Forster

Gahnia javanica Mor. Verz. Zoll. Pfl. 98. 1845-6; F. Muell. in Trans. Roy. Soc. Vict., n.s. 1(2): 36. 1889; C. B. Clarke in Kew Bull. 1899: 114. 1899; Valck. Suring. in Nova Guin. Bot. 8: 708. 1912.

Gahnia javanica Mor. var. *paupercula* Kükenth. in Engl. Bot. Jahrb. 69: 260. 1938, in Bull. Jard. Bot. Buitenz. III, 16: 307. 1940, in Fedde, Repert. 52: 91. 1943.

Gahnia javanica Mor. var. *longearistata* Kükenth. in Bull. Jard. Bot. Buitenz. III, 16: 307. 1940, in Fedde, Repert. 52: 89. 1943.

Gahnia javanica forma *paupercula* (Kükenth.) Kükenth. apud Benl in Bot. Archiv 40: 173. 1940.

NETHERLANDS NEW GUINEA: 9 km. NE. of Lake Habbema, *Brass* 10749, Oct. 1938, alt. 2800 m., several large clumps (1.8-2 m.) on a native clearing in the forest; 6 km. NE. of Lake Habbema, *Brass* 10661, Oct. 1938, alt. 3000 m., associated with subalpine shrubs on open treeless areas of wet sandy or peaty soil down to about 2800 m. alt.; Lake Habbema, *Brass* 9047, Aug. 1938, alt. 3225 m., abundant on lake shores and drier grasslands, scattered through shrubberies and thickets of peaty ridges (achenes yellow; forms large brownish tussocks); Mt. Wilhelmina, 11 km. NE. of top, *Brass & Meyer-Drees* 9704, Sept. 1938, alt. 3400 m., in grassy valley; Mt. Wilhelmina, 7 km. NE. of top, *Brass & Meyer-Drees* 9989, Sept. 1938, alt. 3560 m., abundant in large clumps in forest glades, grassy borders and open grasslands (fruit yellow).

PAPUA: Central Division: Crest of main Owen Stanley Range, *W. MacGregor*, June 1889 (herb. Melbourne); Murray Pass, Wharton Range, *Brass* 4552, June-Sept. 1933, alt. 2840 m., vary abundant in open grasslands (grows in dense tussocks 25-30 cm. diam.; flowering stems yellow; seeds shining pale brown). Eastern Division: Summit of Mt. Dayman, *W. E. Armit, Jr.*, in 1894 (herb. Melbourne).

Widely spread through Malaysia. *Brass* 4552 was cited with the original description of *G. javanica* var. *longearistata*, but the specimens seen do not well agree with the description, since the lower glumes are at most only very shortly awned. *Gahnia javanica* var. *paupercula* appears to be founded on small reduced specimens with scanty inflorescences. I have not seen the type (*Carr* 15237), nor any specimen which agrees with the character of a 4-noded panicle with solitary or binate partial panicles. Armit's collection, cited by Benl, l.c., under forma *paupercula*, has partial panicles up to 5 per node. *Brass* 8477 was cited by Kükenthal (1943, op. cit., 91) under *G. javanica* var. *paupercula*, and on p. 81 under *G. Sieberiana* Kunth. All the material I have seen under this number belongs to *G. Sieberiana*.

The New Guinea material seen by me covers a range of variation from the small reduced plants of *Brass* 4552 (46-50 cm. high with binate or ternate partial panicles) to the large plants of *Brass* 10749 (at least 1.3 m. high, but up to 2 m., according to the collector's notes, with 3-4-nate partial panicles), but all appears to me to represent a single taxonomic entity. From available descriptions, the Javanese plants differ only in having more numerous partial panicles at each node of the inflorescence, but I have seen only one rather unsatisfactory specimen.

Gahnia aspera (R.Br.) Spreng. Syst. Veg. 2: 114. 1825; F. Muell. Pap. Pl. 2: 69. 1890; Kükenth. in Fedde, Repert. 52: 92. 1943.

Lampocarya aspera R.Br. Prodr. 238. 1810.

PAPUA: Western Division: Tarara, Wassi Kussa R., *Brass* 8418, Dec. 1936, in light rain-forests, clumps 1-1.5 m. high; Tarara, Wassi Kussa R., *Brass* 8750, Jan. 1936, "flowering material of no. 8418"; Mai Kussa R., *W. MacGregor*, Feb. 1890, clay soil with eucalypts (herb. Melbourne); Daru Island, *Brass* 8445, April 1936, abundant with *Scleria* sp. as ground cover in transition mangrove — rain-forest.

In New Guinea known only from the Western District of Papua; elsewhere known from eastern Australia, Polynesia, and parts of Malaysia and Japan. All Brass's collections were cited by Kükenthal.

Gahnia Sieberiana Kunth, Enum. Pl. 2: 332. 1837; Kükenth. in Fedde, Repert. 52: 80. 1943.

Gahnia tetragonocarpa Boeck. in Linnaea 38: 347. 1874; Benl in Bot. Archiv 40: 221. 1940.

NETHERLANDS NEW GUINEA: Balim R., Brass 11765, Dec. 1938, alt. 2100 m., plentiful in *Vaccinium* scrubs, on infertile sandy soil (stem-forming species in clumps 2-2.5 m. high; stem and older (erect) branches covered with dry persistent bases of leaves; nuts red).

PAPUA: Western Division: Tumbuke, Wassi Kussa R., Brass 8477, Dec. 1936, savannah-forests, clumps of several erect stems to 1 m. long, 4 cm. diam.

Brass 8477 was cited by Benl, l.c., and Kükenthal, l.c., though Kükenthal also cites this number under *G. javanica* var. *paupercula*. *G. Sieberiana* is elsewhere known from eastern Australia and New Caledonia. *Brass 11765* has more acute and slightly larger nuts than most of the Australian specimens I have seen, measuring 3.7-4 mm. long and 1.5-1.8 mm. wide.

Remirea Aublet

Remirea maritima Aubl. Pl. Guian. 1: 45, t. 16. 1775; K. Schum. in Notizbl. Bot. Gart. Mus. Berlin 2: 98. 1898; K. Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 198. 1901; Rehd. in Jour. Arnold Arb. 14: 65. 1933; Ohwi in Bot. Mag. Tokyo 56: 209. 1942.

Remirea maritima Aubl. var. *pedunculata* (R.Br.) Benth. Fl. Austral. 7: 347. 1878; K. Schum. & Hollr. Fl. Kaiser Wilhelmsl. 25. 1889; Valck. Suring. in Nova Guin. Bot. 8: 708. 1912; Kükenth. in Engl. Bot. Jahrb. 59: 53. 1924, in Fedde, Repert. 53: 207. 1944; H. Pfeiff. in Fedde, Repert. 29: 184. 1931.

Remirea pedunculata R.Br. Prodr. 236. 1810.

Duval-Jouvea maritima (Aubl.) Palla in Rechinger, Denkschr. Math.-Naturw. Kais. Akad. Wiss. Wien 89: 500. 1913.

NORTH-EAST NEW GUINEA: Constantinhafen (Madang), *Hollrung* 506, in 1887, sandy beach (herb. Melbourne).

PAPUA: Eastern Division: Bomgwina, *Brass* 1614, June 1926, abundant on low sand-dunes.

A pan-tropical strand plant. Brass's collection, the only one yet known from Papua, was cited by Rehder, l.c. Brown, Bentham, and Kükenthal, ll.c., distinguished the Australian and Malaysian plant on the grounds that the culm is well exserted from the leaves, and this is indeed often the case, but among the Australian plants seen by me in the field there is every gradation from entirely included to well exserted culms, even on the same plant.

Rhynchospora Vahl

Rhynchospora rubra (Lour.) Makino in Bot. Mag. Tokyo 17: 180. 1903; Kükenth. in Engl. Bot. Jahrb. 59: 82. 1924; Ohwi in Bot. Mag. Tokyo 56: 204. 1942.

Rhynchospora Wallichiana Kunth, Enum. 2: 289. 1837; Valck. Suring. in Nova Guin. Bot. 8: 706. 1912.

Rhynchospora Wallichii (Nees) K.Schum. in K.Schum. & Hollr. Fl. Kaiser Wilhelmsl. 25. 1889, apud Warb. in Engl. Bot. Jahrb. 13: 266. 1891; K.Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 198. 1901.

Schoenus ruber Lour. Fl. Cochinch. 1: 41. 1790.

Morisia Wallichii Nees in Edinb. New Phil. Jour. 17: 265. 1834.

NORTH-EAST NEW GUINEA: Augusta (Sepik) R., *Hollrung* 835 (herb. Melbourne).

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7845*, Sept. 1936, scattered over wet savannahs and grass plains; Gaima, Lower Fly R. (east bank), *Brass 8352*, Nov. 1936, open savannah-forest, common on moister soils (det. Kükenthal); Dagwa, Oriomo R., *Brass 5997*, Feb.-March, 1934, alt. 40 m., abundant on damp slopes and flats in savannah forest and on open country (erect, yellow green; inflorescence brown); Wuroi, Oriomo R., *Brass 5707*, Jan.-March 1934, alt. 10-30 m., abundant on lower savannah ridges; Wuroi, Oriomo R., *Brass 5709*, Jan.-March, 1934, alt. 10-30 m., abundant on gray soil savannah ridges; Tarara, Wassi Kussa R., *Brass 8640*, Jan. 1937, savannah forests, common on acid gray soils; Mai Kussa R., *W. MacGregor* in 1890 (herb. Melbourne). Eastern Division: Sudest Island, *W. MacGregor* in 1889 (herb. Melbourne).

New for Papua; widely spread in the warmer parts of the Old World.

Rhynchospora heterochaeta S. T. Blake in Proc. Roy. Soc. Queensl. 51: 47. 1940.

PAPUA: Western Division: Wuroi, Oriomo R., *Brass 5730*, Jan.-March 1934, alt. 10-30 m., plentiful on damp ground on savannahs; Daru Island, *Brass 6405*, March 1936, common on swampy gray soil in savannah-forests (inflorescence brown, plant stiff, glossy green) (det. Kükenthal).

New for New Guinea; previously known from Queensland, Northern Territory, Java and Philippine Islands. *Brass 5730* was cited by Kükenthal under *R. longisetis* R.Br. subsp. *exserta* (C. B. Clarke) Kükenth., comb. nova, in Bull. Jard. Bot. Buitenz. III, 16: 303. 1940. This combination is based on *R. exserta* C. B. Clarke, an allied species with stouter, much longer hypogynous bristles and a stout style-base as broad as the nut. At least some, if not all the other collections cited by Kükenthal, i.c., with the exception of the one from North Australia (the type of *R. exserta*) belong to *R. heterochaeta*. The remarks also refer to *R. heterochaeta*. *Brass 5730* was also cited under the same trinomial in Engl. Bot. Jahrb. 70: 463. 1940.

Rhynchospora corymbosa (L.) Britton in Trans. N. Y. Acad. Sci. 11: 84. 1892; Kükenth. in Engl. Bot. Jahrb. 59: 52. 1924.

Rhynchospora aurea Vahl, Enum. 2: 229. 1806; F. Muell. Pap. Pl. 1: 74. 1876; K. Schum. & Lauterb. Nachtr. Fl. Deutsch. Schutzgeb. Südsee 60, 1905; Valck. Suring. in Nova Guin. Bot. 8: 706. 1912.

Scirpus corymbosus L. Cent. Pl. 2: 7. 1756.

PAPUA: Western Division: Lake Daviumbu, *Brass 7633*, Sept. 1936, abundant on floating islands in lake (leaves smooth and shining, upper surface showing a bluish metallic sheen). Central Division: Koitaki and Sogere, *C. T. White* 274, July-August, 1918, in wet ground; Port Moresby, *Goldie* (herb. Melbourne); near Port Moresby, *Edelfeldt* 208 in 1884 (herb. Melbourne).

SOLOMON ISLANDS: San Cristobal: Magoha R., *Brass 2750*, Aug. 1932, in clumps 1.5 m. high on 20 ft. silt banks, common.

Pantropical, but apparently not previously recorded for the Solomon Islands.

Rhynchospora triflora Vahl, Enum. 2: 232. 1806.

PAPUA: Western Division: Gaima, Lower Fly R. (east bank), *Brass 8356*, Nov. 1936, occasional in shallow swamps in savannah forest.

New for New Guinea; previously recorded from Ceylon and Tropical America, though there is also a specimen from Malaya in herb. Brisbane (Pahang: Tasek Bera, *M. R. Henderson* in Singapore Field no. 24101, October 1930; distributed from the Botanic Gardens, Singapore, as *Rhynchospora glauca* Vahl).

Rhynchospora Brownii R. & S. Syst. 2: 86. 1817; Ohwi in Bot. Mag. Tokyo 56: 205. 1942.

Rhynchospora laxa R.Br. Prodr. 230. 1810; non Vahl.

Rhynchospora chinensis Nees & Meyen ex Nees in Wight, Contrib. 115. 1834.

Rhynchospora glauca Vahl var. *chinensis* (Nees & Meyen) C. B. Clarke in Hook.f. Fl. Brit. Ind. 6: 671. 1894, quoad syn.

NETHERLANDS NEW GUINEA: Balim R., Brass 11742, Dec. 1938, alt. 1800 m., common in grass on sandy, long deforested slopes; Balim R., Brass 11815, Dec. 1938, alt. 1600 m., common grass associate on sandy, long deforested slopes; 9 km. NE. of Lake Habbema, Brass 10725, Oct. 1938, alt. 2800 m., several slender clumps in a native clearing.

PAPUA: Central Division: Urunu, Vanapa Valley, Brass 4790, July-Aug. 1933, alt. 1900 m., scattered in small clumps on open grasslands.

New for Papua. Spread over Malaysia and the warmer parts of Asia and Australia. It has commonly been identified with the American *R. glauca* Vahl and was referred to this species by Rendle in Gibbs, Phyt. Fl. Arfak Mts. 91. 1917, and by Kükenthal in Engl. Bot. Jahrb. 69: 259. 1938. From the description, *R. glauca* var. *condensata* Kükenth., l.c., (*R. Brownii* var. *condensata* (Kükenth.) Ohwi, l.c.) appears not to be taxonomically different. *Rhynchospora glauca*, of which the legitimate name is *R. rugosa* (Vahl) Gale in Rhodora 46: 275. 1944, differs from the plant of the Eastern Hemisphere in having smaller spikelets and smaller more distinctly rugose nuts with an acute style-base. *Rhynchospora glauca* var. *chinensis* (Nees) C. B. Clarke is founded nomenclaturally on *R. chinensis* Nees, but the description and specimens are of a different plant for which the legitimate name appears to be *R. japonica* Makino in Bot. Mag. Tokyo 17: 184. 1903. It is apparently this plant which Ohwi, l.c., refers to "Rhynchospora chinensis Nees et Meyen ex Nees in Wight, Contr. (1830)- 115, emend. Böcklr. in Linnaea 37 (1873) 586." But Boeckeler's "emendation" does not alter the fact that (nomenclaturally at least) the concept of the species still rests on the type of Nees & Meyen.

QUEENSLAND HERBARIUM,

BRISBANE, QUEENSLAND, AUSTRALIA.

ON THE CONTROL OF DESTRUCTIVE INSECTS IN THE HERBARIUM

E. D. MERRILL

ONE PROBLEM with which most curators of herbaria are concerned is the protection of the collections under their charge against the depredations of destructive insects. The chief offender is the cigarette or tobacco beetle, known in botanical circles as the herbarium beetle, *Lasioderma serricorne* (Fabr.). There are other offenders such as the drug-store beetle, *Stegobium paniceum* (Linn.), but the *Lasioderma* is the most common one. Whatever means prove to be effective in controlling or eliminating the distinctly serious herbarium beetle, will, in general, apply to all other insects that are destructive to stored botanical specimens.

Lasioderma serricorne (Fabr.) is of cosmopolitan distribution, infesting tobacco wherever it is stored. Regarding it, Mallis* says: "The foods upon which it feeds are legion, and a few of these are rice, ginger, raisins, pepper, dried fish, dates, belladonna, drugs, seeds, and pyrethrum powder. They like older tobaccos apparently because they possess a strong odor." Apparently cured tobacco is its most favored food, or at least one of its most favored ones. The life history of the insect is completed in from 70 to 90 days. In temperate climates the insects swarm first in May and again in August. In some parts of the United States there may be three generations in a year; in tropical regions there are as many as five or six overlapping generations within a year. In the humid tropics and even in the warm humid parts of the southeastern United States destruction of herbarium material by these insects is much greater than in cooler regions. However, in heated buildings it is surmised that breeding may take place throughout the year, as is the case in the tropics. The eggs hatch in from six to ten days. The larval stage lasts from five to ten weeks; it is in this stage that herbarium specimens are damaged. At temperatures of about 60° F. the larvae become dormant and may then hibernate. The prepupal and pupal stages last from two to three weeks. Adult beetles may live from three to four weeks. This brief outline is given because of its importance in reference to control by fumigation or by other means. Single fumigations at long intervals are ineffective.

In herbarium practice, from a historical standpoint, controls have taken the form of tight cabinets, sometimes difficult to attain when wood is used, as is generally the case; by actual poisoning of the specimens; and by fumigation. In some institutions repellents are used to a certain degree. Any experienced curator will realize that such controls are only in part effective, for there is always the human element to consider. To keep any

* Mallis, A. Handbook of pest control. 340. 1945.

herbarium free from the depredations of the herbarium beetle and other destructive insect pests involves constant attention. Not infrequently, in little consulted material, the actual destruction of important specimens may reach distinctly large proportions before an infestation is detected.

In earlier years arsenic was effectively utilized, but its use has long since been abandoned because it is a cumulative poison, and in too many cases arsenic poisoning developed among herbarium workers because of their exposure to arsenic dust. Today the most generally used poison is a saturated alcoholic solution of corrosive sublimate to which phenol is sometimes added. This is a very poisonous mixture and has to be handled with great discretion; mercury is also a cumulative poison. It is a well known fact that even when specimens are dipped in the solution and redried before mounting; or when the mounted specimens are sprayed with the solution, or it be painted over the material with a soft brush, permanent protection is not attained. In the course of time the corrosive sublimate becomes inert. When this happens fumigation and re-poisoning are necessary. The treatment is expensive in time and in material, and cannot be considered as efficient. Not infrequently specimens that have been thoroughly poisoned with corrosive sublimate are utterly destroyed by the herbarium beetle. Unfortunately, when specimens are poisoned it may give responsible curators a false sense of security.

At the Gray Herbarium and at the Arnold Arboretum specimens are not poisoned, dependence being placed on tight steel cases combined with fumigation when necessary. The first tight steel cases in botanical history was the beginning of the extensive installation of excellently designed ones at the Gray Herbarium in 1905, followed by the Arnold Arboretum installation in 1908-09. Since the first installation of steel cases in Cambridge the use of them has been greatly extended, but as yet in the majority of the large herbaria of the world dependence is still placed on wooden cases, which, unfortunately, are not always too tight.

It is, in some herbaria, standard practice to fumigate all cases at least once each year. Theoretically with modern tight steel cases, an herbarium should be reasonably free from infestation by the herbarium beetle and similar pests; practically this is not the case for by one means or another gravid female beetles will gain access to stored material; naturally the case doors have to be opened very frequently, and sometimes, through carelessness, they may remain open for relatively long periods of time. With unpoisoned or even poisoned material in storage in the cases this is an invitation to future trouble.

The basic installation at the Arnold Arboretum is represented by an extensive series of modern steel cases. As noted above none of the specimens are poisoned. A decade ago the herbarium beetle infestation here was very extensive throughout the building, mature beetles, pupae and larvae occurring in great abundance in all parts of the large collection; and this in spite of the fact that a few years earlier the entire building had been closed, sealed as tightly as possible, and fumigated with hydrocyanic

acid gas. The situation in 1936 was so critical and destruction so great that one large room was sealed and refumigated with hydrocyanic acid gas. All of the steel cases were fumigated individually, and this fumigation was repeated several times. Through this fumigation campaign naturally not all of the viable eggs, larvae, pupae, and mature beetles were destroyed, but the number of insects was very greatly reduced.

Realizing that fumigation alone, unless repeated at frequent intervals, was not to be depended upon, any more than when all specimens were poisoned with the corrosive sublimate solution, repellents in the form of naphthalene flakes and paradichlorobenzene were placed in each case. In the steel cases this mixture, about two thirds naphthalene and one third paradichlorobenzene was placed in muslin bags, a bag reasonably full of the mixture placed in each case, in an upper pigeon-hole. For the cartons* (and actually in excess of 3,000 of these are now in use for temporary storage of both mounted and unmounted material) a paper flap was pasted on the bottom near the back of each carton, under which was placed a large handful of the repellent. It has been current practice to renew the repellent once each year. It is admitted that the use of these substances may be objectionable for occasionally an individual may be allergic to one or both of them; yet with the cases closed the odor in the building is never strong, and is normally in no way objectionable. In fact the odor is scarcely noticeable at any time except near a recently opened case.

There is, of course, always the chance of reinfestation of stored collections even if the specimens be poisoned, even if the cases are tight, and even if repellents are used. Naturally the combined naphthalene-paradichlorobenzene fumes within the cases are not in sufficient concentration to be lethal to either the eggs, the larvae, the pupae, or the adult insects. It is, however, a manifest fact that the odor is very objectionable to the insects and that the gravid female will always choose unprotected material as a place for depositing her eggs, if there be any choice.

It is not claimed that the extensive fumigation campaign in 1936-37 destroyed all of the thousands of herbarium beetles that at that time thoroughly infested the reference collections at the Arnold Arboretum. With large collections of incoming material constantly being received from all parts of the world there was always the chance of reinfestation. As a matter of fact the greatest danger of reinfestation is returned in loans from other institutions, and duplicate material received from such institutions as exchanges. In some recently returned loans the destruction of the specimens while away for study purposes was so great that some drastic step seemed to be called for. For the present this has merely taken the form of a sticker, printed in red ink and attached to all outgoing loan forms, reading:

"Important Notice

In recent years we have had the sad experience of finding that certain returned loans of important historical botanical material were badly in-

* Merrill, E. D. An economical herbarium case. *Torreya* 26: 50-54, fig. 1-2. 1926.

fested with herbarium beetles. In one particular case the essential parts of many important specimens were utterly destroyed during the time the material was on loan, reducing their value to a minimum. Please safeguard this loan against the ravages of herbarium beetles throughout the period of the loan by the liberal use of insect repellents such as naphthalene or paradichlorobenzene. *These specimens have not been poisoned and hence are particularly subject to the ravages of herbarium pests.*"

Our actual loans within the past decade have varied from a minimum of about 1000 to a maximum of 4000 or an average of about 2500 mounted sheets per year. All material borrowed from other institutions for study purposes, and these borrowings averaged 3000 per year during the past decade, is fumigated immediately on receipt of a shipment. In the decade the total receipt of specimens from all sources, including duplicates, approximate 430,000 to which may be added about 65,000 sheets in the form of borrowed specimens and returned loans, or a grand total of nearly 500,000 specimens, all to be considered as potential sources of reinestation of our herbarium by the herbarium beetle.

In current practice all incoming material is thoroughly fumigated, whether this consists of new collections as received from the field, exchanges from other institutions, purchased material, borrowed sheets and returned loans. All material, as mounted, is placed in tight cases well supplied with the repellent. Even before a distribution into the herbarium such material, after being placed in family arrangement, is refumigated. Such steps have been considered to be necessary to avoid adding infested specimens to the reference collections. Special care has been taken to see that the doors of all cases be kept tightly shut except as it was necessary to open them when material was being studied, removed, or added. A study collection taken out even for a period of only a few weeks, is always fumigated before the specimens are returned to permanent storage.

It is now about eight years, since these regulations went into full force. In that period no staff member, visiting botanists or students have reported seeing live beetles, larvae, or pupae in the building. This is, indeed, a very striking contrast to a decade ago when the infestation was very great; so great that one could find quantities of live beetles, larvae, and pupae, more or less embedded in the strips of felt against which the doors of the steel cases close. In this period the number of staff members who use herbarium material all or a part of their time has varied from the neighborhood of eight to ten individuals; and this takes no account of scores of visiting botanists and students who have consulted our material. All investigators were requested to watch for signs of insect damage and for live insects, and if any of the latter were observed, to report the matter at once; there have been no reports of infestation in the period covered. The herbarium now contains approximately 700,000 mounted sheets, with many additional thousands of unmounted specimens in storage, with vast collections of undistributed duplicate material of one type or another. None of the specimens is poisoned. Considering the tremendous infestation of a

decade ago, and the situation that still exists in certain other large herbaria, this is indeed a remarkable record.

It is a well known fact that the herbarium beetle is very selective. Entire families of plants are more or less immune to their attacks, although it is admitted that they will destroy flowers of most species in most families, as well as soft fruits and soft vegetative parts. Curiously the Gramineae, which yields most of the forage on which herbivorous mammals subsist, are, in general, free from the depredations of the herbarium beetle except in those genera which have pithy stems more or less charged with sugar or starch, such as *Zea*, *Saccharum*, and allied genera. Another monocotyledonous group that is also remarkably free from their depredations is the Cyperaceae. In those families having sclerophyllous or leathery tough leaves, such as most of the Coniferae, the Palmae, as to their leaves, the Myrtaceae, the Lauraceae, the Guttiferae, many genera of the Ericaceae, and numerous other families, damage is normally slight except to the flowers. In the tropics, even when all material had been poisoned with the corrosive sublimate solution, I have noticed serious damage even to the sedges and some grasses, as well as to the ferns and fern allies, mosses, and lichens. One may assume that no single natural group of plants is wholly immune to attack. Certain it is that the flowers of all or most species are vulnerable.

Generally speaking certain natural families of flowering plants are peculiarly susceptible to damage or destruction by herbarium insects. Whether or not the gravid females are attracted by certain odors is not known, but it is suspected that this is the case. It is a well known fact that stored herbarium material in certain families is characterized by distinctive odors, such as the Caprifoliaceae, Umbelliferae, Araliaceae, Labiateae, Compositae, etc. all highly susceptible groups. However, distinctive odors are not in general associated with material representing other preferred families such as the Solanaceae, Scrophulariaceae, Capparidaceae, Cruciferae, Asclepiadaceae, Apocynaceae, Moringaceae, Tropaeolaceae, Papavaraceae, Ranunculaceae, Nymphaeaceae, Liliaceae, Araceae, and certain genera of the Leguminosae and Rosaceae, all groups that are especially attractive to the herbarium beetle larvae. It is to be noted that the majority of the species in most, but not all, of these families are predominantly herbaceous. It seems highly probable that the gravid female insects may be attracted by certain glucosides, alkaloids, or food elements in representatives of the above families, as well as by distinctive odors. Whatever the attraction is, it is clear that the families listed above are the preferred ones, and stored specimens representing them are those most frequently damaged or even destroyed by these herbarium pests. It may be noted that the same elements (glucosides) which give the characteristic taste to most representatives of the Cruciferae, occur also in the Tropaeolaceae and the Moringaceae; all or most of the representatives of these three families of plants are peculiarly susceptible to attack by the herbarium beetle. Usually it is largely the flowers and the tender leaves that

are destroyed; but in unprotected Umbelliferae often the whole plant is devoured, even the somewhat lignified stems of certain species. At any rate an experienced and observant curator can cite cases of utter destruction of important material in such families as those above listed through the unchecked ravages of active and rapidly increasing colonies of herbarium beetles.

This selectiveness of the gravid females as to preferred food plants gave me an idea which I put into practice following the last comprehensive fumigation of our herbarium cases nine years ago. A selection was made from common species to which the herbarium beetle is notably partial, such as *Asclepias*, *Apocynum*, representatives of the milky Compositae such as *Sonchus* and *Taraxacum*, and selected genera in the Solanaceae (including *Nicotiana*), Umbelliferae, Cruciferae, Papaveraceae, Labiateae, and Scrophulariaceae. Wherever possible selection was made on the basis of tenderness of vegetative parts and abundance of flowers. Quantities of roughly dried herbarium specimens were prepared. This material was placed loose on specimen sheets and tied in unwrapped bundles about six inches thick. Twelve of these bundles of preferred plants, "bug traps" if you wish, were numbered, dated, and placed in strategic places in all rooms where herbarium material was stored or handled. About four times each year these "bug traps" are picked up, fumigated, redated, and returned to their positions in the building. The evidence is that, following fumigation, the use of repellents, plus the installation of the "bug traps," is what has kept a once very badly infested, large herbarium, and one in which none of the specimens are poisoned, entirely free (as far as our observations go) from infestations of the herbarium beetle for a period of eight years. In that period the only material that has suffered has been that loaned to specialists in other institutions for study purposes.

There is another group of much smaller insects which are destructive in a limited sense, which many curators overlook or perhaps ignore. These are the so-called book lice, representatives of the Psocidae, which thrive on pollen, even when the specimens have been poisoned by corrosive sublimate. Thus it is that pollen experts, turning to this or that herbarium for material, are sometimes disappointed by discovering that these nefarious little insects have anticipated them by destroying all of the pollen grains in both open and unopened anthers. They are controlled even easier than the herbarium beetle by the use of repellents. It is possible that certain Thysanoptera do a certain amount of damage to stored herbarium material on occasion, especially where the humidity is high. These, and all other insects which thrive on dried herbarium specimens are easily controlled by the simple methods outlined above.

It is admitted that the installation of "bug traps" which I advocate, may be a potential source of reinfestation of stored herbarium material, whether this be poisoned or unpoisoned. There is thus a certain human element in the picture. However, if all the "bug traps" be picked up at regular intervals, a minimum of four times a year at three months inter-

vals, and thoroughly fumigated before they are replaced, there is no danger. In practice it would doubtless be advisable to replace the material that make up the "bug traps" occasionally; here this has been done only once since the first installation was made eight years ago.

I believe that our experience over a decade, with not a single live beetle, pupa, or grub reported in the last eight years, rather definitely demonstrates the efficacy of this very simple and relatively inexpensive method of eliminating these herbarium pests. The scheme is practicable, efficient, and what is more, inexpensive; in fact much less expensive in time and in material than the current practice, in some large herbaria, of poisoning all material with corrosive sublimate before the mounted sheets are distributed into the herbarium, to say nothing of repeated fumigations. Perhaps the very simplicity of the plan will militate against its general use, but definitely it is worth a thorough trial. About the only chances of reinestation, once a herbarium is free from these destructive pests, would be to forget to renew the repellent in the cases (this should be done once a year), to forget to pick up and fumigate all the "bug traps" at proper intervals (once in about three months); to fail to fumigate all incoming material, including exchanges, recently collected material coming in from the field, borrowed material, and returned loans. A potent source of reinestation is material that has been exposed in institutions where it is known that bad infestations exist, including exchanges, loans, and borrowed specimens. Admittedly my observations are based entirely on empiricism, i.e., observation; but never-the-less the simple scheme works. I unhesitatingly recommend it to all curators of herbaria who are faced with the really serious problem of protecting their collections against the ravages of destructive insects.

From our experience it is not necessary to look upon the presence of from few to many of these destructive insects in any herbarium as a necessary evil and one that cannot be avoided. It has been demonstrated, through our experience over a decade, that the herbarium beetle and other secondary herbarium pests can be thoroughly and economically controlled by the simple method outlined above, and this without the use of poison, or poisonous gases other than the desirable preliminary fumigations. Not one of our numerous steel cases has been fumigated in eight years, or since the "bug traps" were installed; and no infestations have been discovered in the thousands of cartons now in use. The entire herbarium, consisting of approximately 700,000 mounted sheets, none of the material poisoned with corrosive sublimate, is now free from infestation, and it is anticipated that it will remain free as long as the present practice of fumigation of all incoming material, free use of repellents, and the maintaining of "bug traps" with their fumigation at regular intervals, is followed.

Father Hugh O'Neill* has demonstrated the fact that heat may be efficiently used in the control of herbarium pests. If the temperature be raised to 140° F. (60° C.) this is sufficient to kill insects in all stages of

* O'Neill, H. Heat as an insecticide in the herbarium. *Rhodora* 40: 1-4. 1 fig. 1938.

development and within a few minutes. Because of the nature of the stored material it takes four or five hours at a temperature of 170° F. (77° C.) to attain this end, as paper is a poor conductor of heat and of course it is necessary to raise the temperature in the center of the bundles to that required for lethal purposes. Most institutions are not equipped to apply this heat treatment, although at the University of Montreal each storage case is equipped with an electrical heating unit. The use of a partial vacuum is very effective in killing insects. Here the initial installation is expensive, and because the bulky herbarium material must be transported to and from the vacuum chamber, the labor costs are high; this same statement applies when herbarium material must be transported to a heat equipped unit.

It is believed that some of the modern insecticides such as DDT may prove to be very efficient either sprayed over the specimens or merely sprayed over the interior surface of the storage units. Father O'Neill reports to me that with sprayed specimens difficulties may develop, for certain individuals are allergic to DDT dust. In one case that he mentioned the difficulties were so great that spraying of specimens has been discontinued and now dependence is placed on spraying the interior of the storage units. Perhaps this spraying of the interior surfaces of the pigeon holes occasionally may suffice; at any rate it is distinctly worth a thorough trial. We do know from our own experience over the past decade that the combination of fumigation, use of repellants, and the installation of "bug traps" is very effective.

I have noted above that there is always the human element to be considered. Unless curators assume their proper responsibilities and keep constantly on the alert for indications of the presence of the herbarium beetles, no matter what system be followed reinfestation may occur at any time during the breeding season of the insects involved. Proper precautions and eternal vigilance on the part of responsible officials is the price that an insect free herbarium exacts. The cooperation of all staff members and of others who have occasion to consult stored material is important, and this whether the specimens be poisoned or not. Whether an infestation be light or severe, it should be attended to immediately once it is discovered. To delay in applying control methods is merely to invite disaster in the form of the destruction of often very valuable and utterly irreplaceable specimens.

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THE NOMENCLATURE OF
THE FLOWERING DOGWOOD AND ITS ALLIES

HIROSHI HARA

DR. MERRILL HAS RECENTLY MENTIONED that the botanist who deals with monographs or local floras should at least take Rafinesque's names into consideration. This statement well applies to the case of modifying the genus *Cornus* in a broad sense. Since Dr. Nakai,¹ in 1909, divided *Cornus* into four genera and then carefully revised his opinion in *Flora Sylvatica Koreana XVI, Cornaceae* (1927), his followers in Japan have been supporting his classification. In 1942 Dr. Hutchinson completely agreed with Dr. Nakai's opinion on this subject, although he unfortunately overlooked Dr. Nakai's second paper, and added two new genera: *Afrocrania*, a monotypic genus from tropical Africa, and *Dendrobenthamia*, a group of the Japanese flowering dogwood.

For a group of the flowering dogwood in North America, both authors adopted *Cynoxylon* Rafinesque (1838) as a generic name, following Small and Britton. It is my opinion,² however, that Rafinesque intended to publish the name *Cynoxylon* as a subgenus of *Cornus*, not as a genus. At first Rafinesque proposed *Cynoxylon* as a section name of *Cornus* in his *Medical Flora* Vol. 1, p. 132 (1828). Then he published it with a formal description on page 59 of his *Alsographia Americana* (1838) as follows:

"257. EUKRANIA Raf. florib. pedicel. umbellatis, . . . trees and plants—Types C. mascula, canadensis and suecica. Krania and Mesomora were grecian names of the Cornel.

"258. CYNOXYLON Raf. (dog-wood) petalis obtusis, florib. sessilib. subcapitatis, involucris 4 phylis coloratis ineq. emarg. fruct. distinctis, oblongis, fol. oppos.—Type C. florida, distinguished since 1828.

"259. BENTHAMIA Lindl. non Rich. Raf. sylv. tel. 817 different *Cynoxylon*, drupis coalitis concretis (syncarpes) ut in *Morus*—Type B. or *Cornus fragifera* Wallich."

On the preceding page of the same work, *Mesomera* and *Kraniopsis* were clearly designated as subgenera of *Cornus*. *Eukrania* and *Cynoxylon* without exact indication have often been considered genera. For the following reasons, it is rather clear, I think, that Rafinesque intended *Cynoxylon* as a subgenus. In the first place, in the index on page 76 of the same work, *Eukrania* and *Cynoxylon* are both written in italics which was explained to denote subgenera. Secondly, he made no binomial combinations under either name. This case has been discussed in detail by Farwell.³ If *Eukrania* and *Cynoxylon* had been considered as genera

¹ NAKAI, *Cornaceae in Japan*. Bot. Mag. Tokyo 23: 35-45. 1909.

² When I investigated this problem in 1940, I came to the following conclusion independently. Through the courtesy of Dr. Merrill, I have now noted the recent discussions on the same subject by Rickett and Farwell published in *Torreya* 42: 11-14, 130, 131. 1942.

by Rafinesque, he would have mentioned at least under *Eukrania* as "Types E. or *Cornus mascula*, . . ." instead of "Types C. mascula, . . ." as in the case of *Benthamia* Lindl., which was clearly regarded as an independent genus. Thirdly, in his *Sylva Telluriana* (p. 130), which was published in the same year as *Alsographia Americana*, he clearly noted under *Benthamia* Lindl. that "very singular G. (= genus) uniting the *Cornides* with *Naucleides*, very near to my subg. *Cynoxylon* of med. fl. 1828." So, according to my interpretation, Rafinesque in 1838 published *Cynoxylon* and *Eukrania* as well as *Mesomera* and *Kraniopsis* as subgenera of *Cornus*. Although Jackson in *Index Kewensis* 1: 689. 1893 listed *Cynoxylon* as a genus, it was not validly published as a genus until Small adopted it in 1903. Therefore, the earliest correct generic name for the flowering dogwood is *Benthamidia* Spach published in 1839 and based on *Cornus florida* L., as Dr. H. N. Moldenke has adopted it.

A group of the Japanese flowering dogwood in Asia, i.e. *Dendrobenthamia* Hutch., differs from the American species of the flowering dogwood by having ovaries and fruits perfectly united into a fleshy globose syncarp. A similar difference is sometimes observed within a single genus, as for example in *Lonicera*, and to my way of thinking it is not sufficient for generic separation, since they agree otherwise in important morphological, anatomical and cytological characters. On this point I quite agree with Dr. Nakai in regarding both the New and Old World species of the flowering dogwood as a single genus, and in recognizing two sections based on fruiting characters. I now propose the following treatment under the generic name *Benthamidia*:

Benthamidia Spach, Hist. Nat. Vég. Phan. 8: 106. 1839, emend. Hara.

Cornus Sect. *Involucratae* DC., Prodr. 4: 273. 1830, pro parte.

Cornus Sect. *Benthamia* (Lindl.) Koehne, Deutsch. Dendr. 435, 438. 1893.

Benthamia Lindley sensu Nakai in Bot. Mag. Tokyo 23: 40. 1909.

Cynoxylon Rafin. sensu Nakai, Fl. Sylv. Korea. 16: 67. 1927.

Benthamidia Sect. 1. *Cynoxylon* (Rafin.) Hara, comb. nov.

Cornus Sect. *Cynoxylon* Rafinesque, Medic. Fl. 1: 132. 1828.

Cornus Subgen. *Cynoxylon* Rafinesque, Alsogr. Amer. 59. 1838.

Benthamidia Spach, l.c. 1839.

Cornus Sect. *Tanycrania* Endlicher, Gen. Pl. 2: 798. 1839, pro parte.

Cornus Gruppe *Benthamidia* (Spach) K. Koch, Dendr. 1: 694. 1869.

Cynoxylon Rafin. ex Jackson, Ind. Kew. 1: 689. 1893; Small, Fl. SE. United States, 854. 1903; Britton, N. Amer. Trees 744. 1908; Hutchinson in Ann. Bot. n.s. 6: 91. 1942.

Cornus Sect. *Discocrania* Harms et *Benthamidia* (Spach) Harms in Nat. Pflanzenfam. III. 8: 267. 1897.

Benthamia Subgen. *Apocarpea* Nakai Sect. *Benthamidia* (Spach) et Sect. *Discocrania* (Harms) Nakai, l.c. 41. 1909.

Cornus Subgen. *Benthamidia* K. Koch ex Schneider, Ill. Handb. Laubh. 2: 453. 1909.

Cornus Subgen. *Discocrania* (Harms) et *Benthamidia* (Spach) Wangerin in Engl. Pflanzenreich IV. 229(Heft 41): 84-86. 1910.

³ FARWELL, *Eukrania* and *Cynoxylon* not genera of Rafinesque. *Rhodora* 34: 29-30. 1932.

1. *Benthamidia florida* (L.) Spach, Hist. Nat. Vég. Phan. 8: 107. 1839.*Cornus florida* L., Sp. Pl. 117. 1753.*Cynoxylon florida* (L.) Rafin. ex Jackson, Ind. Kew. 1: 689. 1893; Hutchinson, l.c. 92. 1942.*Benthamia florida* (L.) Nakai in Bot. Mag. Tokyo 23: 41. 1909, in nota.

DISTRIBUTION: Eastern North America (Maine, S. Ontario, Minn. to Florida, Texas).

Benthamidia florida f. *rubra* (André) Hara, comb. nov.*Cornus florida* var. *rosea* Carr. & André in Rev. Hort. 1891: 369. 1891.*Cornus florida* var. *rubra* André in Rev. Hort. 1894: 500, t. 1894.*Cynoxylon floridum* var. *rubrum* (André) Moldenke in Bull. Torrey Bot. Club 60: 56. 1933.*Benthamidia florida* var. *rubra* (André) Moldenke in Torreya 34: 8. 1934.*Cornus florida* f. *rubra* (West) Palmer & Steyermark in Ann. Missouri Bot. Gard. 22: 612. 1935.*Benthamidia florida* f. *pendula* (Dipp.) Hara, comb. nov.*Cornus florida* *pendula* Anon. in Wien. Ill. Gart.-Zeit. 12: 508. 1887.*Cornus florida* var. *pendula* Dippel, Handb. Laubh. 3: 244. 1893.*Cynoxylon floridum* var. *pendulum* (Dipp.) Moldenke, l.c. 56. 1933.*Benthamidia florida* var. *pendula* (Dipp.) Moldenke, l.c. 8. 1934.*Benthamidia florida* f. *pluribracteata* (Rehder) Hara, comb. nov.*Cornus florida* f. *pluribracteata* Rehder in Jour. Arnold Arb. 7: 243. 1926.*Benthamidia florida* f. *xanthocarpa* (Rehder) Hara, comb. nov.*Cornus florida* var. *xanthocarpa* Rehder, Man. Cult. Trees Shrubs 673. 1927.*Cornus florida* f. *xanthocarpa* Rehder, l.c. ed. 2, 688, 1940.*Benthamidia florida* var. *urbiniana* (Rose) Hara, comb. nov.*Cornus urbiniana* Rose in Contrib. U. S. Nat. Herb. 8: 53. 1903.*Cornus florida* var. *urbiniana* (Rose) Wangerin in Engl. Pflanzenreich IV. 229 (Heft 41): 87. 1910.*Cornus florida* subsp. *urbiniana* (Rose) Rickett in Bull. Torrey Bot. Club 72: 223. 1945.

DISTRIBUTION: Mexico.

2. *Benthamidia Nuttallii* (Audubon) Moldenke in Phytologia 1: 167. 1935.*Cornus Nuttallii* Audubon, Birds N. Amer. t. 367. 1837; ed. nov. 4: 313, t. 279. 1842; Torrey & Gray, Fl. N. Amer. 1: 652. 1840.*Cynoxylon Nuttallii* (Audubon) Shafer in Britton & Shafer, N. Amer. Trees 746, fig. 684. 1908; Hutchinson, l.c. 92. 1942.*Benthamia Nuttallii* (Audubon) Nakai in Bot. Mag. Tokyo 23: 41. 1909, in nota.

DISTRIBUTION: Western North America (British Columbia to S. California).

3. *Benthamidia disciflora* (Moc. & Sessé ex De Candolle) Hara, comb. nov.*Cornus disciflora* Moc. & Sessé ex De Candolle, Prodr. 4: 273. 1830.*Cornus grandis* Chamisso & Schlechtendal in Linnaea 5: 171. 1830.*Benthamia disciflora* (Moc. & Sessé) K. Koch, Hort. Dendr. 285. 1853.*Benthamia disciflora* (Moc. & Sessé) Nakai et *grandis* (Cham. & Schlecht.) Nakai in Bot. Mag. Tokyo 23: 41. 1909, in nota.*Cynoxylon disciflorum* (Moc. & Sessé ex De Candolle) Hutchinson, l.c. 91. 1942.

DISTRIBUTION: Central Mexico and Costa Rica.

Benthamidia disciflora var. *floccosa* (Wangerin) Hara, comb. nov.*Cornus floccosa* Wangerin in Fedde, Rep. Nov. Sp. 6: 101. 1908.*Cornus disciflora* var. *floccosa* (Wanger.) Standley in Field. Mus. Publ. Bot. 8: 321. 1931.*Cynoxylon floccosum* (Wanger.) Hutchinson, l.c. 91. 1942.

Cornus disciflora f. *floccosa* (Wanger.) Rickett in Bull. Torrey Bot. Club 72: 223. 1945.

DISTRIBUTION: Mexico.

Benthamidia Sect. 2. *Cephalocrania* (Hance) Hara, comb. nov.

Benthamia Lindley in Bot. Reg. 19: t. 1579. 1833; non A. Richard (1828), nec Lindley (1830).

Cornus Sect. *Cephalocrania* Hance in Jour. Linn. Soc. 13: 105. 1873, in textu.

Cornus Sect. *Benthamia* (Lindl.) C. B. Clarke in Hooker, Fl. Brit. Ind. 2: 745. 1879.

Cornus Sect. *Benthamia* (Lindl.) Koehne, Deutsch. Dendr. 435. 1893.

Benthamia Subgen. *Syncarpea* Nakai Sect. *Eubenthamia* Nakai in Bot. Mag. Tokyo 23: 41. 1909.

Cornus Subgen. *Benthamia* Benth. & Hook. ex Schneider, Ill. Handb. Laubh. 2: 454. 1909.

Cornus Subgen. *Benthamia* (Lindl.) Wangerin in Engl. Pflanzenreich IV. 229(Heft 41): 88. 1910.

Cynoxylon Sect. *Benthamia* (Koehne) Nakai, Fl. Sylv. Korea. 16: 68. 1927, cum Subsect. *Japonicae* Nakai.

Dendrobenthamia Hutchinson in Ann. Bot. n.s. 6: 92. 1942.

4. *Benthamidia japonica* (Sieb. & Zucc.) Hara, comb. nov.

Benthamia japonica Sieb. & Zucc., Fl. Jap. 1: 38, t. 16. 1836; Nakai in Bot. Mag. Tokyo 28: 314. 1914, cum α *typica*, β *minor* et γ *exsucce* Nakai.

Cornus Kousa Buerger ex Miquel in Ann. Mus. Bot. Lugd.-Bat. 2: 159. 1865, pro syn.; Hance in Jour. Linn. Soc. 13: 105. 1873; Masamune & Nakamura in Trans. Nat. Hist. Soc. Formosa 33: 56, fig. 1, 2. 1943.

Cornus japonica Thunb. sensu Koehne, Deutsch. Dendr. 438. 1893; non Thunberg 1784.

Benthamia Kousa (Buerg.) Nakai in Bot. Mag. Tokyo 23: 41. 1909.

Benthamia viridis Nakai, Chosen-Shokubutsu 1: 426. Mar. 1914, in textu jap., in Bot. Mag. Tokyo 28: 314. Nov. 1914.

Cynoxylon japonica (Sieb. & Zucc.) Nakai in Bot. Mag. Tokyo 31: (148). 1917, in textu, Fl. Sylv. Korea. 16: 69, t. 19-22. 1927, cum var. *typica*, f. *minor*, var. *exsucce* et var. *viridis* Nakai.

Cynoxylon Kousa (Buerg.) Nakai ex Mori, Enum. Pl. Corea. 275. 1922, nom. seminud.

Dendrobenthamia japonica (Sieb. & Zucc.) Hutchinson, l.c. 93. 1942.

DISTRIBUTION: Honshu, Shikoku, Kyushu, Loochoo, Formosa, and Central and Southern Korea.

Benthamidia japonica var. *chinensis* (Osborn) Hara, comb. nov.

? *Benthamia chinensis* Hort. ex Lavalée, Arb. Segrez. 129. 1877, pro syn.

Cornus Kousa Buerg. sensu Rehder in Pl. Wilson. 2: 577. 1916; Bean in Curtis's, Bot. Mag. t. 8833. 1920; Hu, Icon. Pl. Sin. 1: t. 42. 1927.

Cornus Kousa var. *chinensis* Osborn in Gard. Chron. ser. 3, 72: 310. 1922; Bean in Kew Bull. 1926: 321, t. 8. 1926; Rehder, Man. Cult. Trees Shrubs 673. 1927.

Cynoxylon sinense Nakai in Jour. Jap. Bot. 15: 741. 1939.

DISTRIBUTION: China (Kiangsu, Chekiang, Anhwei, Hupeh, Kiangsi, Hunan, Kwangtung, Shensi, Szechuan, Kweichow, Yunnan).

Benthamidia japonica var. *angustata* (Chun) Hara, comb. nov.

Cornus Kousa Buerg. var. *angustata* Chun in Sunyatsenia 1: 285. 1934.

DISTRIBUTION: China (Kwangtung).

5. *Benthamidia hongkongensis* (Hemsl.) Hara, comb. nov.

Benthamia japonica Sieb. & Zucc. var. *sinensis* Bentham in Hooker, Jour. Bot. & Kew Misc. 4: 165. 1852.

Cornus hongkongensis Hemsley in Jour. Linn. Soc. 23: 345. 1888; Chun in Sun-yatsenia 1: 281. 1934.

Benthamia hongkongensis (Hemsl.) Nakai in Bot. Mag. Tokyo 23: 41. 1909, in nota.

Cynoxylon hongkongensis (Hemsl.) Nakai in Jour. Jap. Bot. 15: 742. 1939.

Dendrobenthamia hongkongensis (Hemsl.) Hutchinson, l.c. 93. 1942.

DISTRIBUTION: China (Chekiang, Kwangtung, Kwangsi, Kweichow, Yunnan) and Indo-China (Tonkin).

Benthamidia hongkongensis var. *gigantea* (Hand.-Mzt.) Hara, comb. nov.

Cornus hongkongensis var. *gigantea* Hand.-Mzt., Symb. Sin. 7(3): 690. 1933.

DISTRIBUTION: China (Yunnan).

6. *Benthamidia ferruginea* (Wu) Hara, comb. nov.

Cornus ferruginea Wu in Bot. Jahrb. 71: 199. 1940.

DISTRIBUTION: China (Kwangtung, Kwangsi).

7. *Benthamidia capitata* (Wall. ex Roxb.) Hara, comb. nov.

Cornus capitata Wallich ex Roxburgh, Fl. Ind. ed. Carey, 1: 434. 1820; Wallich, Pl. Asiat. Rar. 3: 10, t. 214. 1832.

Benthamia fragifera Lindley in Bot. Reg. 19: t. 1579. 1833.

Benthamia capitata (Wall.) Nakai in Bot. Mag. Tokyo 23: 41. 1909, in nota.

Cynoxylon capitata (Wall.) Nakai in Cat. Semin. Hort. Bot. Univ. Tokyo, 1918: 22. 1918, nom. nud., in Jour. Jap. Bot. 15: 742. 1939.

Dendrobenthamia capitata (Wall.) Hutchinson, l.c. 93. 1942.

DISTRIBUTION: China (Hupeh, Kiangsi?, Hunan, Kwangtung?, Kwangsi, Szechuan, Kweichow, Yunnan), Indo-China (Tonkin, Laos), Upper Burma and Himalaya.

Benthamidia capitata var. *khasiana* (Clarke) Hara, comb. nov.

Cornus capitata var. *khasiana* C. B. Clarke in Hooker, Fl. Brit. Ind. 2: 745. 1879.

DISTRIBUTION: Himalaya (Khasia).

Benthamidia capitata var. *mollis* (Rehder) Hara, comb. nov.

Cornus capitata var. *mollis* Rehder in Pl. Wilson. 2: 579. 1916.

?*Cornus capitata* var. *hypoleuca* Léveillé, Cat. Pl. Yunnan 59. 1916.

DISTRIBUTION: China (Hupeh and Yunnan?).

For those botanists who are unfamiliar with Dr. Nakai's paper in 1927, a few additional notes to Dr. Hutchinson's article will be interesting. The earliest author who adopted a pre-Linnean name, *Chamaepericlymenum*, is Hill, and he used it for the dwarf honeysuckle as a generic name in the British Herbal p. 331 (1756). *Macrocarpium officinale* (Sieb. et Zucc.) Nakai is a native of Korea, and in Japan it is only cultivated in the garden.

In completing this paper, the author wishes to express his deepest gratitude to Dr. Merrill for his very kind and helpful advice.

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